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HOST-DETERMINED MORPHOLOGICAL VARIATIONS IN LECANIUM CORNI[1,2]

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INTRODUCTION

THE EFFECT of the host species on the insect phenotype may be said to be: (1) physical, when the host causes the insect to develop structurally to conform to certain structural peculiarities of its own, and (2) physiological, when, consumed as food, it affects certain physiological and morphological characteristics of the insect.

The physical effect is exemplified in the case of sessile insects, such as scales, by distortions of bodily forms induced by their living in furrows in the bark or by their adapting themselves to parts of plants which do not allow for normal expansion and growth.

Another physical effect of the host is that which influences the size of certain insects because of limitations in the amount of available food, owing to the nature of the host species. Thus, insects infesting seeds, such as certain weevils, may develop to only a small fraction of their normal size because the seeds of the host species which they happen to infest are too small to afford adequate nourishment for normal development. The same may be said of parasites attacking insect-host species of different sizes.

The *physiological* effect of the host, according to the foregoing classification, is exemplified by certain morphological variations of *Lecanium corni* Bouché on its different host species, which will be discussed at length. *L. corni* was selected for this work because it presents such a conspicuous variety of forms on its various hosts.

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DESCRIPTION OF LECANIUM CORNI

Although an early, detailed anatomical study of the genus *Lecanium* Burmeister was made by Thro (1903),[4] much confusion has resulted because of the instability of the characters used in the classification of this group (Sanders, 1910). Early workers were not judicious in their choice of structural characters for the classification of *Lecanium* species. Host

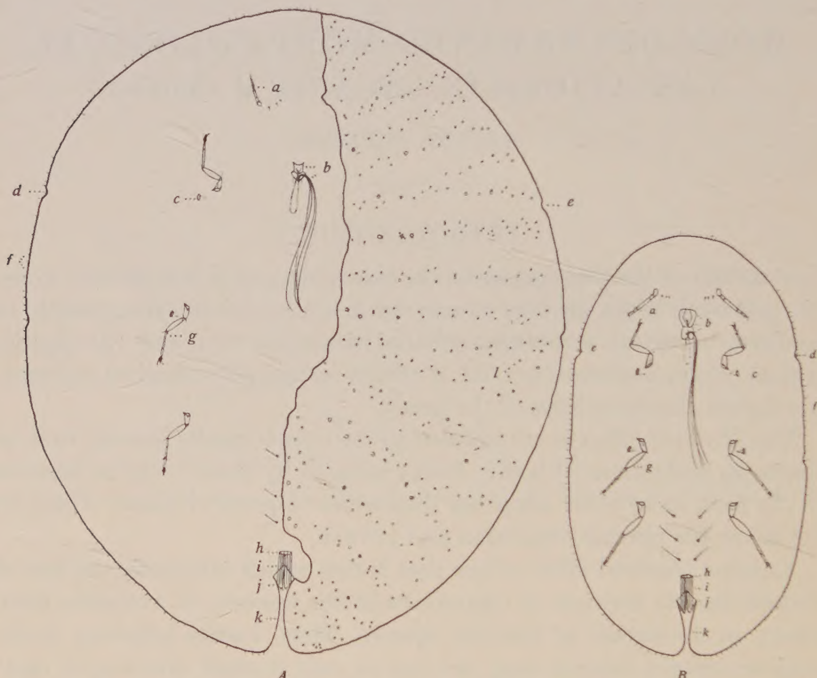

Fig. 1.—*Lecanium corni* Bouché: *A*, ventral surface of adult female; *B*, ventral surface of second instar. *a*, Antenna; *b*, mouth parts; *c*, spiracle; *d*, spiracular spines; *e*, spiracular depression; *f*, marginal spines; *g*, leg; *h*, anal ring; *i*, spines on anal ring; *j*, anal plates; *k*, anal cleft; *l*, derm pores. (× 20.)

plant, color, size, and shape were considered the most important characters for use in classification. The futility of using such indefinite and instable characters for classification is now apparent.

In common with other species of the genus, *Lecanium corni* is characterized superficially by the convexity of its body and by the brownish color of its derm. Like other species, also, it has an anal cleft, at the base of which is located a pair of anal plates (fig. 1).

[4] See "Literature Cited," at the end of the paper, for complete data on citations, which are referred to in the text by author and date of publication.

More specifically the structural characters of *Lecanium corni*, as it occurs on its more common hosts, such as *Prunus* sp., may be briefly described as follows:

Adult Female.—Size 2.5 to 3.0 mm × 4.0 to 6.0 mm; outline from nearly circular to ovoid or cymbiform, moderately convex, dried specimens having a dorsal ridge from which striations radiate to the sides; color reddish brown to chocolate-brown. Antennae usually 7-segmented, 200 to 340 microns long, the 3rd segment being the longest, the 2nd and 4th, 1st and 7th, and 5th and 6th segments being subequal. Legs 325 to 425 microns long, having a fairly definite arrangement of setae (from a lateral aspect usually 5 may be seen on the coxa, 1 on the trochanter, 3 on the femur, 2 on the tibia, and 3 or 4 on the end of the tarsus), with 2 tenent hairs attached on each side of the end of the tarsus, projecting well beyond the claws, the upper tenent hairs longest, practically uniform in thickness throughout, the plates almost twice as long as broad, the caudo-lateral margin little longer than the cephalo-lateral, with 4 fringe setae arranged in two pairs, with 4 apical and 2 subapical setae on each plate. Anal ring with 8 hairs. Derm pores of two fairly distinct sizes, usually single, but often in pairs or multiple, arranged in irregular rows radiating from the center to the margins. Marginal spines short and stout, about 80 microns apart; outer spiracular spines more than half as long as the middle spiracular spine.

Lecanium corni has but a single generation a year. In southern California the eggs hatch in early spring. *L. corni* is an active insect for a day or two after hatching. It has the usual appendages, which become fully developed in the second instar (fig. 1, *B*). In the third and last instar, the insect increases in the size of its body and proboscis only. The antennae and legs of the mature insect cannot be seen from the dorsal aspect, being concealed by the body of the insect.

MORPHOLOGICAL VARIABILITY OF LECANIUM CORNI

Many observations have been made concerning the variations in the form and coloration of *Lecanium corni* as it occurs on its many hosts. Ferris (1920) was impressed by the great variation in the external form among individuals of this species. After examining scales from a number of hosts, he states, "There is a very considerable diversity in appearance among specimens from these various hosts, ranging from the large pruinose form on elm to a very small and shiny form on *Arbutus*. . . ."

Marchal (1908) was able to prove that *Lecanium robiniarum* Douglas, described from specimens on black locust, was merely a host form of *L. corni*. He found that when specimens of *L. corni* were transferred from peach trees to a young locust tree isolated from other trees of the same species, their progeny assumed the typical *robiniarum* form. Only four individuals survived to full maturity out of the thousands that hatched from the eggs of the adults transferred from peach trees, but

these had the large size, dark coloring, and the specific appearance of *L. robiniarum.* Each individual produced thousands of eggs.

Marchal stated that the foregoing experiment was proof that *Lecanium robinarium* is only a variety of *L. corni* by adaptation to the *Robinia* and therefore designated it by the name *L. corni* var. *robiniarum.* It is now known by that name among European entomologists.

Voukassovitch (1930) also produced specimens of *Lecanium corni* var. *robiniarum* by transferring *L. corni* from plum to locust. Other interesting transformations were found by Voukassovitch to be caused by other host species in further translocation experiments.

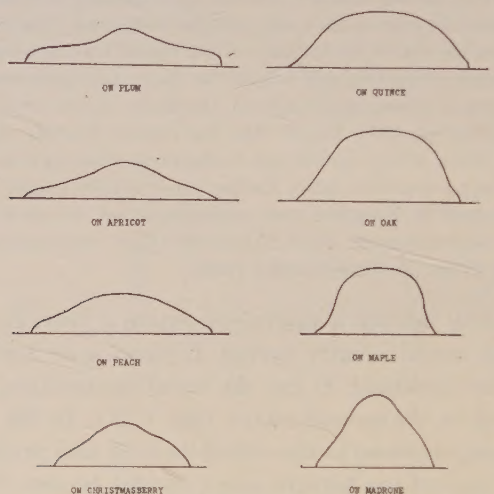

Fig. 2.—Cross sections of dried specimens of *Lecanium corni* Bouché, showing differences in form on various host species. (× 5.)

Sanders (1909) made some translocation experiments with *Lecanium corni* and stated that "Remarkable changes are wrought in the individual scales when transferred to a new host plant."

The very marked differences in external appearances occurring among the scales on different species of hosts are shown in figure 2. This figure indicates the gradation in convexity, which is apparent upon examination of dried specimens from a lateral aspect, from the large, very flattened individuals found on prune, *Prunus domestica* L., to the extremely convex or sometimes globular ones found on madrone, *Arbutus Menziessii* Hook. In general, the greatest similarity exists between individuals from hosts which are most closely related—compare the cross sections on the various species of *Prunus* in figure 3 with those on other genera.

An interesting variation from the usual form of *Lecanium corni* is presented by specimens that developed on maple, *Acer macrophyllum* Pursh. On this host they are small, very convex, smooth, and of a distinctly light-brown color. In figure 2 is shown the form of the insect from a lateral aspect. This is probably the insect that Ehrhorn (1898) described as *L. crawii,* specimens of which he took from maple in northern California. This insect can be differentiated from the more common forms of *L. corni* only in superficial appearance. As far as the characters upon which the identification of the species is based are concerned, the form on maple is typically *L. corni.* As in other cases of dispute over the specific identity of scale insects, only translocation of the insects can definitely prove whether the morphological peculiarities of the insect are genetic or merely the result of the influence of the host. Much of this type of work would have been done already were it not for the difficulty of transferring *L. corni* from one host to another in sufficient numbers to carry an experiment to conclusion.

THE INFLUENCE OF HOST-DETERMINED PHENOTYPIC VARIATIONS ON THE SYNONYMY OF LECANIUM CORNI

Lecanium corni has been reported in various countries in Europe and North America on about a hundred species of host plants. In many cases it has been described as a separate species on the basis of specimens taken from only a single host. This led to a considerable synonymy of the species. Although *L. corni* on locust was sufficiently different in appearance from the same species on peach, for instance, to be determined as a separate species, *L. robiniarum* (see p. 615), Marchal (1908) noted that all gradations between *L. corni* on locust and *L. corni* on peach could be found in nature. Thus the form named *L. vini* Bouché, which occurs on grapes, and the form named *L. wistariae* Sign., which occurs on *Glycine* (soybean), often closely resemble the form on locust. *L. crawii* Ehrh., which is now considered a form of *L. corni,* was named a new species on the basis of specimens taken from only one host, *Acer macrophyllum* (see Ehrhorn, 1898). Likewise, the form on *Adenostoma* has been called *L. adenostomae* Kuwana. Steinweden (1930), after a careful study of specimens from both maple and *Adenostoma,* as well as other hosts on which *L. corni* assumes an unusual superficial appearance, says, "Although there are some differences in external appearance, the morphological differences are too slight to separate them from typical *corni.* No further classification seems possible until careful breeding work on a variety of hosts is carried out."

Marchal (1908) has listed nine European species as synonyms of *Lecanium corni,* to which Sanders (1909) has added twenty-six American species. In working out the synonymy of *L. corni,* Sanders studied the types of all the species he listed as synonyms except four, and in these cases similar topotypic material was examined. He believed, with Marchal, that a very important source of confusion to systematists working on *Lecanium* was the variation in the form and appearance of these insects on their different host plants. Thus he stated:

> Moreover, within the last decade or two, many species have been described . . . with but little regard for the individual variations which are bound to appear in insects so absolutely dependent upon the kind and condition of their host plants as are the sedentary scale-insects. It is most unreasonable to expect to find a perfectly formed and fully developed *Lecanium* or *Pulvinaria* on a twig or stem of 1/16-inch diameter on a starved plant, when the normal form would appear only on the flat surface of a leaf or a large stem in vigorous growth.

Marchal (1908), after commenting on the effect of the host species and the structures of the different parts of the host on the form of *Lecanium corni,* remarks,

> Tous ces stades et tous ces aspects divers formaient un ensemble fort disparate, bien fait pour modérer les tendances dangereuses de ceux qui, se cantonnant dans leur cabinet de travail au lieu d'observer et d'experimenter à l'air libre, multiplient les especes à l'infini, sans avoir sous les yeux les pièces indispensables pour étayer leur opinion.

The tendency to create synonyms is probably as great among systematists working on other coccids as among those working on the scale insects. Ferris (1918) has long admonished entomologists concerning the unreliability of such superficial and variable characters as waxy secretions and antennal graphs as criteria for the identification of mealybugs because of the great variation found in this group. A large percentage of the synonymy of insects, individuals of which are largely confined to a single host, may be attributable to variations caused by the nature of the host. Other environmental factors, such as temperature and humidity, may be of some importance, but they affect large areas in a more or less uniform way and are more apt to cause an intergradation of phenotypic characters from one area to another. This type of variation is perhaps satisfactorily incorporated into the modern species concept.

BIOMETRICAL EXPERIMENTS WITH LECANIUM CORNI

Methods.—After many unsuccessful trials at transferring *Lecanium corni* from host to host, the writer endeavored to determine by statistical studies to what extent, if any, the morphology of the insect is influenced by its various host species as they occur in nature. An attempt was made

to discover whether insects from plants of a given species from identical and different environments presented any variations in structure. Since with a single exception, the writer has found *L. corni* only on Christmasberry (*Photinia arbutifolia* Lindl.) and apricot (*Prunus Armeniaca* L.) in southern California, the statistical studies were largely confined to the insects as they occur on these two hosts.

Christmasberry trees heavily infested with *Lecanium corni* were selected in three widely separated environments, Waterman Canyon, Glendale, and Livermore. Waterman Canyon is located in the San Bernardino Mountains, California, at an elevation of about 3,500 feet; Glendale is near the coast in Los Angeles County, California; and Livermore is also in the coastal region, but about 400 miles north of Glendale. The latter is not in the native range of Christmasberry, but the tree had been transferred there from the mountains. Two trees were selected for experimentation in Waterman Canyon in order to determine whether or not trees of the same species growing in the same environment could differently affect the morphology of *L. corni*. One tree was selected in each of the other two environments.

The tree environments present a great diversity of climate in temperature, humidity, length of seasons, and perhaps other factors. Waterman Canyon is in a region of repeated snows during the winter months, and, owing to its elevation, is cool the year round. Glendale is in a mild climate, never experiencing snowfall, and with high temperatures during the summer months. Livermore, which is the farthest north of the three environments, has a climate warmer than Waterman Canyon but colder than Glendale, and is, of the three, the most humid and also the most uniform the year round.

Mature gravid females of *Lecanium corni* were taken from the leaves of the trees during the spring and summer and were cleared and stained according to the following technique: The specimens were first boiled in a 10 per cent caustic-potash (KOH) solution for 10 minutes, then washed in acidulated water, and immersed in saure fuchsin stain for 20 minutes. They were then washed in water to remove the excess stain, immersed in 35 per cent, 60 per cent, and 95 per cent alcohol successively, passed through carbolxylol, and mounted in balsam. Over 2,000 insects were stained in this manner during the course of the investigation.

Variations in Size and Structure of the Antennae.—The expression of the sizes of the various segments of the antenna in microns or other suitable units of measurement is known as the antennal formula. Graphically expressed, these dimensions are known as an antennal graph. Antennal formulas and graphs were once used as specific criteria, and

are still extensively employed in the description of insects. Cockerell (1913) mentioned the value of antennal segments in species determination of coccids if sufficient numbers were examined and formulas or graphs were formed so as to include the extremes of variation. Hollinger (1917) and Brain (1915) made use of antennal graphs in their works on scale insects and discussed at length the methods of constructing the graphs. Ferris (1918) discusses antennal graphs in relation to several species of *Pseudococcus,* but says, "Even though it be true that the average graph of any species is relatively constant, this does not aid in the identification of nonaverage individuals. . . . The graphs are neither sufficiently distinctive nor sufficiently constant to be of value in separating species."

Whether antennal formulas and graphs are satisfactory or not in the differentiation of species, they are nevertheless useful in depicting in a comprehensible way the differences existing among the individuals on different host plants provided a large number of antennal measurements are used.

A large number of antennae from scales taken from Christmasberry in Waterman Canyon, Glendale, and Livermore were measured in order to determine the differences in the size and structure of the antennae of the insects on a given host under identical and under different environments. By dividing the mean length of the antenna by the mean length of a single segment (in the present case the fourth segment), a ratio is established which may be called the structural ratio of the antennae of *Lecanium corni* on the particular host plant in question. Variations in the structure of the antennae effected by the host plant may then be measured by the variations in the structural ratio. Table 1 gives the structural ratios of the antennae of *L. corni* taken from different trees of Christmasberry.

The differences in the size and structure of the antennae (see table 1) are within the limits of experimental error. This experiment implies that the mean size and structure of the antennae of *Lecanium corni* on different trees of Christmasberry remain practically constant under similar or diverse environmental conditions.

Specimens of *Lecanium corni* were also selected from three environments—Fullerton, Anaheim 1, and Anaheim 2—on the twigs of apricot. In Fullerton, California, the first environment, the insects were selected from two trees about 25 feet apart. The second and third environments were about 2 miles apart in Anaheim, California, and are designated as Anaheim 1 and Anaheim 2. Here the insects were selected from a single tree. The differences in the environmental conditions of the regions in

TABLE 1

Size and Structural Ratio of the Antennae of Lecanium Corni Taken from Different Trees of Christmasberry and of Apricot

Environment	Number of antennae	Mean length of antenna, microns	Mean length of 4th segment, microns	Structural ratio
From different trees of Christmasberry				
Waterman Canyon, tree 1	662	291.92±0.44*	52.36±0.17	5.57
Waterman Canyon, tree 2	658	291.34±0.45	52.77±0.15	5.52
Glendale	391	296.71±0.51	54.10±0.17	5.48
Livermore	96	295.83±2.02	53.10±0.40	5.57
From different trees of apricot				
Fullerton, tree 1	663	239.25±0.65	38.49±0.12	6.21
Fullerton, tree 2	545	234.90±0.46	37.92±0.16	6.19
Anaheim 1	129	243.54±0.87	40.05±0.31	6.08
Anaheim 2	170	239.60±0.77	38.40±0.27	6.24

* Throughout the tables in this paper, mean and probable error of the mean are given, the latter calculated from the formula, probable error $= \frac{\pm 0.6745\sigma}{\sqrt{n}}$.

which specimens of *L. corni* were taken from apricot are not so great as the differences in the environmental conditions of the regions in which the insects were taken from the Christmasberry. With the exception of the two adjacent trees in Fullerton, however, the trees are sufficiently

TABLE 2

Size and Structural Ratio of the Legs of Lecanium Corni Taken from Different Trees of Christmasberry and of Apricot

Environment	Number of legs	Mean length of leg, microns	Mean length of tibia, microns	Structural ratio
From different trees of Christmasberry				
Waterman Canyon, tree 1	134	399.78±1.20	77.22±0.35	5.18
Waterman Canyon, tree 2	105	394.05±1.21	75.60±0.38	5.21
Glendale	189	398.64±0.61	77.54±0.23	5.14
Livermore	100	394.50±1.38	76.44±0.41	5.16
From different trees of apricot				
Fullerton, tree 1	97	362.35±1.04	65.30±0.38	5.55
Fullerton, tree 2	105	359.85±1.07	64.33±0.33	5.59
Anaheim 1	121	366.95±0.78	64.34±0.23	5.70
Anaheim 2	144	360.49±0.88	64.05±0.24	5.63

distant from one another to obviate the possibility of their harboring populations of scales of immediately common ancestry.

Data for scales on apricot similar to those secured in the preceding experiment are also summarized in table 1. As in the case of *Lecanium corni* on Christmasberry, a considerable uniformity in the structure of the antennae of insects on different trees of the same species was found.

Variations in Size and Structure of the Legs.—By use of the ratio of

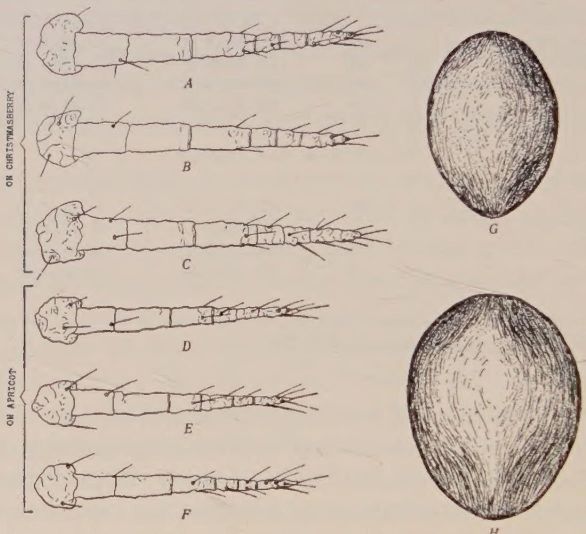

Fig. 3.—Left, antennae of *Lecanium corni* Bouché from different hosts and different environments: *A, B, C,* on Christmasberry—*A* from Waterman Canyon, *B* from Glendale, and *C* from Livermore; *D, E, F,* on apricot—*D* from Fullerton, *E* and *F* from Anaheim. (*A–F*, × 150.) Right, dorsal aspect of *L. corni*, showing relative size of an average individual on Christmasberry (*G*) and on apricot (*H*). (*G, H,* × 6.) Note that although the insects on Christmasberry are smaller than those on apricot, they have larger antennae.

the length of the leg to the length of the tibia as a structural ratio, a uniformity is observed among individuals of *Lecanium corni* taken from Christmasberry in different environments, as is shown in table 2 for Waterman Canyon, Glendale, and Livermore.

In a similar way, it can be shown that the ratio of the length of the forelegs to the length of the tibiae is also practically constant when the specimens are taken from different apricot trees in similar and diverse environments. The data showing this morphological constancy are also given in table 2.

By comparing the structural ratios of the antennae and legs of *Lecanium corni* on Christmasberry with the structural ratios of the antennae and legs of *L. corni* on apricot, the variations in the structure of these appendages caused by the two host species can be readily appreciated. The structural ratios for the antennae of the scales on the former host range from 5.48 to 5.57, while on the latter host they range from 6.08 to 6.24 (table 1). Corresponding ratios for legs range from 5.14 to 5.21 on Christmasberry, and on apricot from 5.55 to 5.70, respectively (table 2).

TABLE 3

MEAN LENGTH OF ANTENNAE, LEGS, AND BODIES OF LECANIUM CORNI ON CHRISTMASBERRY AND APRICOT

Host	Number of individuals	Mean length of antennae, microns	Mean length of legs, microns	Mean length of body, microns
Christmasberry	1,049	292.99±0.26	397.25±0.66	3,942.24±15.65
Apricot	1,046	238.32±0.28	361.17±0.50	5,278.68±15.31

When the *t* test for significance (Snedecor, 1937) was applied, the differences in the means of the structural ratios between the insects on the two host species were found to be highly significant.

Variations in Body Proportions.—While the insects taken from Christmasberry have longer antennae and legs than those taken from apricot, they are nevertheless much smaller in total length, measured from the anterior to the posterior tip of the derm. This striking structural inconsistency is shown in table 3 and, for antennal length and body length, in figure 3.

The ratio of the difference of the means to its own standard deviation is especially significant as indicating the probability of the statistical significance of the difference of the means, that is,

$$\frac{M_1 - M_2}{\sigma_{(M_1-M_2)}} \text{ when } \sigma_{(M_1-M_2)} = \sqrt{\sigma_1{}^2 + \sigma_2{}^2}$$

The following figures are computed in the above manner, and show the high degree of statistical significance of the data: For length of the antennae on the two hosts,

$$\frac{M_1 - M_2}{\sigma_{(M_1-M_2)}} = 97.62$$

The corresponding figures for the length of the legs and the length of the bodies are, respectively, 24.05 and 41.18.

According to conventional standards in taxonomic work, if the source of the insects were not known, the structural differences between *Lecanium corni* on Christmasberry and *L. corni* on apricot shown by the foregoing data might legitimately be construed to indicate that the insects on these two hosts are distinct species. The translocation experiments cited

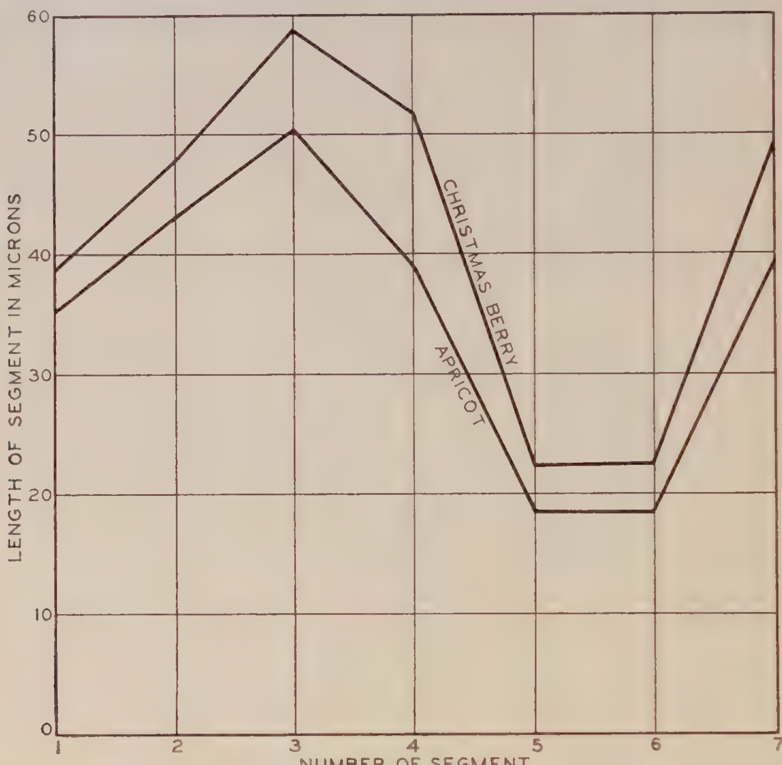

Fig. 4.—Differences in antennal structure of *Lecanium corni* on Christmasberry and apricot, caused by the host species.

later prove definitely, however, that the differences found between the insects on these two hosts are caused by the differences in the plants themselves.

Graphs showing the differences in the structure of the antennae and legs of *Lecanium corni* on Christmasberry and on apricot are shown in figures 4 and 5. It is obvious from an examination of the graph that the ratios of the segments to one another are different on the two hosts. The differences in the antennae of the insects taken from Christmasberry and from apricot are also shown in figure 3.

It may be argued that differences in the structure of the appendages may occur concomitantly with differences in their length, irrespective of the species of host from which the insects were taken, but we have not found this to be true. Appendages of the smallest insects on Christmasberry, which averaged the same in length as the average appendages of the insects on apricot, did not have the structural peculiarities of the

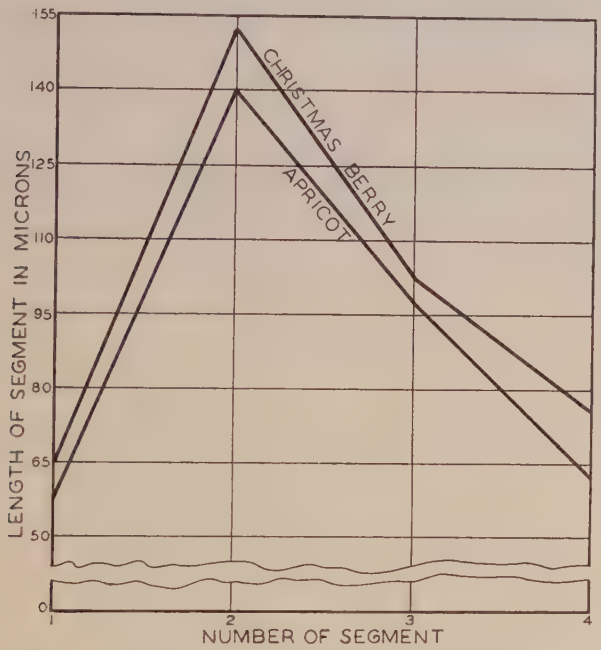

Fig. 5.—Difference in structure of foreleg of *Lecanium corni* on Christmasberry and on apricot.

latter, but conformed closely to the structure of the average appendages of the insects on Christmasberry. Structural differences, then, are independent of the absolute dimensions of the appendages, but are due rather to the differences in the species of hosts from which the insects bearing the appendages were taken.

The relative sizes of the antennae of *Lecanium corni* on Christmasberry and on apricot are graphically illustrated in figures 6 and 7. When individuals from these two hosts are combined in one frequency distribution for antennal length, a markedly bimodal curve results (fig. 6). When the distributions for the two hosts are plotted separately, the two curves closely approximate the "normal curve," and overlap only slightly (fig. 7).

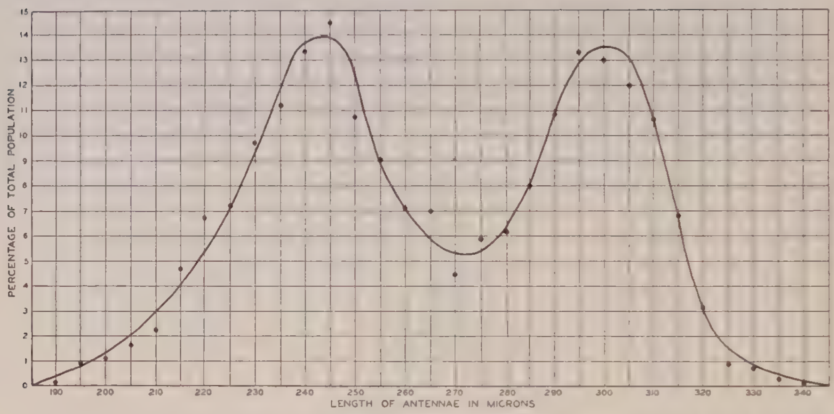

Fig. 6.—Bimodal curve resulting when individuals of *Lecanium corni* from two host species, apricot and Christmasberry, are combined into one frequency distribution for antennal length.

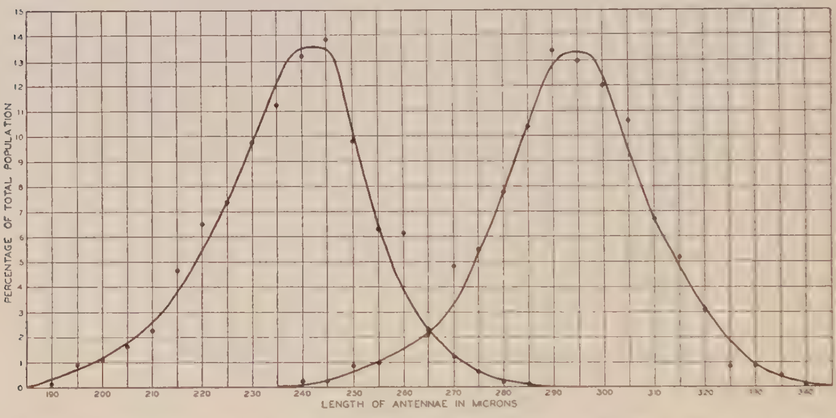

Fig. 7.—Slightly overlapping "normal curves" resulting when individuals of *Lecanium corni* from apricot (left) and Christmasberry (right) are placed in their respective frequency distributions for antennal length.

TRANSLOCATION EXPERIMENTS

Technique.—The effect of the host species on insect morphology has been determined in the past by biometrical methods and by translocation experiments. In the case of *Lecanium corni*, the latter method presents certain difficulties. Repeated attempts to transfer *L. corni* in nature from one host plant to another over a wide range of temperatures and with many species of host plants have been successful in only a single instance. Translocation was effected more successfully in the laboratory.

The method of translocation in either case has consisted of attaching twigs of one host heavily infested with gravid females or newly hatched larvae of *Lecanium corni* to another host. When the twigs of the first host begin to dry, the young larvae (those hatched before the twig was transferred or those resulting when eggs of the females on the old host hatch) crawl off and attach themselves to their new host.

Thousands of insects have thus migrated in the course of the experiments from Christmasberry and apricot to Christmasberry, apricot, prune, peach, locust, willow, potato, and *Malva*. On all but the last three hosts, the transferred larvae have developed in the usual manner throughout the summer and fall on the leaves of their hosts, but have usually failed to make a successful migration from the leaves to the twigs and branches before the abscission of the leaves at the approach of winter—even when they are transferred from one plant to another of the same species.

The difficulty encountered in transferring *Lecanium corni* is not surprising, in view of the fact that Voukassovitch (1930) reports that only two or three individuals per thousand were successfully transferred by him in Yugoslavia, where conditions for survival appear to be unusually favorable.

Apricot to Christmasberry.—In the spring of 1933, large numbers of apricot twigs heavily infested with gravid *Lecanium corni* were fastened to uninfested Christmasberry shrubs in Orange County Park, California. Enormous numbers of young scales settled on the Christmasberry leaves, and of these a considerable number migrated to the branches in the fall. In the spring of 1934, 21 mature scales were found on the shrubs infested the previous fall. These were removed, cleared, and stained according to the method previously mentioned, and microscopic measurements were made of antennae and legs of these individuals. The mean antennal formula in microns was found to be 40.6, 47.9, 60.8, 55.0, 23.9, 24.2, 46.5, and the leg formula, 66.8, 159.9, 109.9, 77.5. By comparing these formulas to corresponding formulas for *L. corni* on Christmasberry, as established by previous investigations (see figs. 4 and 5), it can be seen that they coincide remarkably well, both in structure and size. The scales transferred from apricot to Christmasberry had developed not the apricot-form characteristics of their progenitors, but the typical characteristics of the Christmasberry form. Because of the tremendous mortality of insects, the possibility of selection is not excluded. However, the mortality appears to be just as great when the larvae are settling on the host plant or host species upon which their progenitors have lived for generations.

Alder to Apricot.—On June 17, 1934, the writer found *Lecanium corni* infesting a number of alder (*Alnus rhombifolia* Nutt.) trees in the upper reaches of San Antonio Canyon in the Sierra Madre Mountains of southern California. These insects were small and very convex in form, a great contrast to the apricot form of *L. corni* (fig. 8). A comparison of

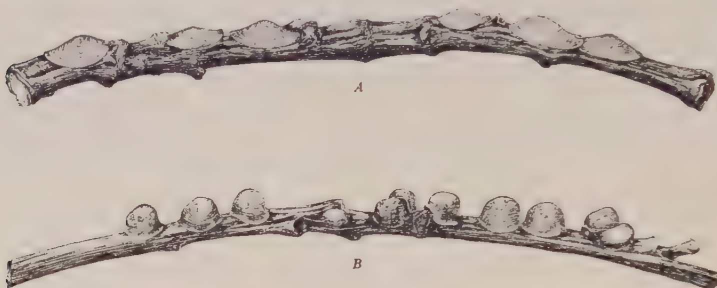

Fig. 8.—Difference in structure of scales on different host species: *A*, *Lecanium corni* Bouché on apricot; *B*, on alder. (× 2.)

the shape of *L. corni* on alder and apricot was made by measuring the height and length of all insects and calculating a structural ratio (fraction of height over length) for the insects on each host. An idea of the difference in the structure of the bodies of the insects on the two host species can be obtained by comparing the structural ratios (see table 4).

TABLE 4

DIFFERENCES IN THE STRUCTURAL RATIOS OF ADULT LECANIUM CORNI, TAKEN FROM ALDER AND APRICOT TREES

Host	Number of individuals	Height	Length	Height / Length
		mm	*mm*	
Alder	200	2.29	3.29	0.696
Apricot	200	2.10	5.27	0.398

By plotting the heights of the scales taken from alder and apricot as ordinates and the lengths as abscissas (fig. 9), it was found that the points representing the individuals from the two hosts were confined to two distinct areas in the coördinate system. Thus again two host forms of a species are structurally distinct, with greater structural differences than are sometimes found between distinct species.

A number of *Lecanium corni* from alder were transferred to apricot trees growing in a laboratory at temperatures varying from 70° to 80° F

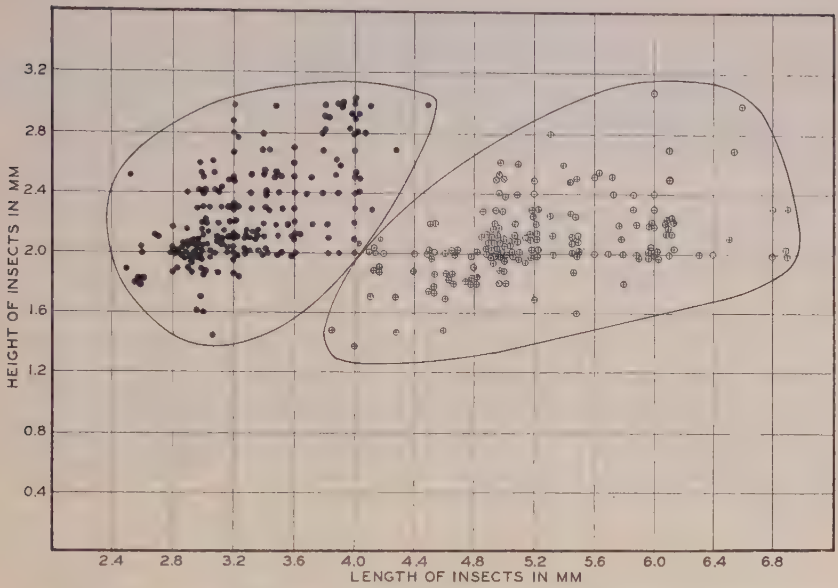

Fig. 9.—Structural difference between *Lecanium corni* Bouché on alder and on apricot: left, points representing the structural ratio of individuals taken from alder; right, points representing the structural ratio of individuals taken from apricot.

Fig. 10.—Progeny of the form of *Lecanium corni* on alder (fig. 8) which were reared in an insectary on apricot. (× 5.)

throughout the life cycle of the insects, and some of these reached maturity in the spring of 1935. These correspond closely in size and structure to scales normally occurring on apricot (fig. 10). Again, variation in structure was definitely correlated with the host species.

SUMMARY

A scale insect, *Lecanium corni* Bouché, was selected as the subject for experimentation on the effect of the host species on the morphology of insects because of the great morphological variation in this species on its various host plants in nature.

A detailed description of *Lecanium corni* is given. Its structural variability is greatly influenced by various host species. Much of the synonymy of *L. corni* has resulted from the confusion arising from its host-determined morphological variability.

On the basis of certain structural ratios, such as the ratio of the length of the antennae to the length of the body, ratios of the lengths of antennae or leg segments to one another or to the length of the entire appendage, and the ratio of the height of the entire insect to its length, certain morphological differences in *Lecanium corni* have been evaluated statistically.

Individuals of *Lecanium corni* taken from apricot (*Prunus Armeniaca* L.) have large bodies and short appendages; those taken from Christmasberry (*Photinia arbutifolia* Lindl.) have small bodies and long appendages. The antenna and leg formulas, which show the ratios of the lengths of the segments of these appendages to one another, are also different on the two hosts. When individuals from the two hosts are combined in one frequency distribution for antennal length, a markedly bimodal curve results. When the distributions for the two hosts are plotted separately, the curves each closely approximate the "normal curve" and overlap only slightly.

Adult insects were transferred from apricot to Christmasberry in the field, and their progeny developed the structural characteristics of the Christmasberry form of *Lecanium corni*.

On alder (*Alnus rhombifolia*) the ratio of height to length of *Lecanium corni* is 0.696; on apricot it is 0.399. Progeny of adult insects transferred from alder to apricot in the laboratory developed the structural characteristics of the apricot form.

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LITERATURE CITED

BRAIN, C. K.
1915. The *Coccidae* of South Africa. Part I. Roy. Soc. So. Africa, Trans. 5 (Part 2): 65–194.

COCKERELL, T. D. A.
1913. *Phenacoccus betheli* again. Canad. Ent. 45:14–15.

EHRHORN, E. M.
1898. New Coccidae. Canad. Ent. 30:244–46.

FERRIS, G. F.
1918. The California species of mealy bugs. 77 p. Stanford Univ. Press, Stanford University.
1920. Scale insects of the Santa Cruz Peninsula. 57 p. Stanford Univ. Press, Stanford University.

HOLLINGER, A. H.
1917. Taxonomic value of the antennal segments of certain Coccidae. Ann. Ent. Soc. Amer. 10:264–71.

MARCHAL, P.
1908. Notes sur les cochenilles de l'Europe et du nord de l'Afrique. Ann. Soc. Ent. France 77:223–309.

SANDERS, J. G.
1909. The identity and syonymy of some of our soft scale-insects. Jour. Econ. Ent. 2:428–48.
1910. A review of the *Coccidae* described by Dr. Asa Fitch. Ent. Soc. Wash. Proc. 12:56–61.

SNEDECOR, G. W.
1937. Statistical methods. 341 p. (See specifically p. 54, 55, and 204.) Collegiate Press, Inc., Ames, Iowa.

STEINWEDEN, J. B.
1930. Characteristics of some of our California soft scale insects (Coccidae). California State Dept. Agr. Mo. Bul. 19:561–71.

THRO, W. C.
1903. Distinctive characteristics of the species of the genus *Lecanium*. New York (Cornell) Agr. Exp. Sta. Bul. 209:201–21.

VOUKASSOVITCH, P.
1930. Sur la polyphagie de la cochenille *Lecanium corni*. Compt. Rend. Soc. Biol. Paris 104:1065–68.

THE ORANGE TORTRIX, ARGYROTAENIA CITRANA

A. J. BASINGER

THE ORANGE TORTRIX, ARGYROTAENIA CITRANA[1,2]

A. J. BASINGER[3]

INTRODUCTION

This paper presents data on the biology and economic importance[4] of the orange tortrix, *Argyrotaenia citrana* (Fernald), which is the most important of several species of small moths, the larvae of which have caused damage for many years to the orange and occasionally to other citrus fruits in southern California. Other species considered to a lesser extent, are *Holcocera iceryaeella* (Riley), *Platynota stultana* Walsingham, and *Pyroderces rileyi* (Walsingham).

SYSTEMATIC POSITION

The orange tortrix is a member of the Tortricidae, which is a family of small Lepidoptera including the leaf-rollers and bud moths. The species was described and placed in the genus *Tortrix* by Fernald in 1889, but its generic position has been somewhat uncertain in recent years. The author follows August Busck[5] of the United States Department of Agriculture, who places it in the genus *Argyrotaenia.*

ORIGIN

Coquillett (1894)[6] suspected that the orange tortrix was imported from some of the Pacific Islands. Prior to the inauguration of the rigid plant-quarantine service in California, it could easily have been brought into this country in the egg, larval, or pupal stage on imported plants. If it is an introduced species, the first stock must have been brought in some

[1] Received for publication May 6, 1938.

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[4] Control is not discussed in this paper, since further experimental work on that phase is still in progress by the Experiment Station. Those interested in a discussion of the control are referred to papers by Basinger and Boyce (1935 and 1936).

[5] Information from personal correspondence with August Busck, October 24, 1936.

[6] See "Literature Cited" at the end of the paper, for complete data on citations, which are referred to in the text by author and date of publication.

years before 1885, for that year marks the first recorded notice of injury to oranges, and it must have been present in some groves in considerable numbers by that time.

The evidence available, on the other hand, seems to indicate that the orange tortrix is a native species which existed here on other host plants long before citrus was introduced into this country. It is not dependent on citrus for existence, since it has a wide range of host plants, on any one of which it can readily complete development. Coquillett (1894) records it as occurring on willow, oak, walnut, and goldenrod, all native plants. The author found it on native *Lotus* sp. at Torrey Pines in San Diego County, in 1926, somewhat removed from any citrus plantings. The fact, also, that it is a host for a number of different species of parasites further supports the idea that it is a native of the extreme southwestern United States and perhaps contiguous Mexico, though no records are known of its occurrence in Mexico.

HISTORY

The first reports of damage to oranges in California by a lepidopterous larva were received by D. W. Coquillett (1894), a representative of the United States Department of Agriculture, in 1885, when he was in southern California carrying on some of the earliest experiments with cyanide fumigation for the control of citrus scale insects. Coquillett sent specimens of the moths to the United States Department of Agriculture, in Washington, where they were recognized as an undescribed species. In 1889 Fernald described the species, naming it *Tortrix citrana*.

In 1894 Coquillett (1894) stated that, judging by the number of letters he received regarding it, the orange tortrix must have been plentiful the previous season, and in 1898 Chappelow (1898) reported it as doing considerable damage in the vicinity of Monrovia. Quayle, in 1910, noted that much injury to oranges occurred from Glendale to Pomona. The first published record of the orange tortrix in Orange County was made by Weldon in 1914, but the species had probably been there for years before it was reported. Quayle again, in 1918, stated that there were heavy infestations in the Pasadena and Alhambra sections.

Since that time, heavy and widespread infestations occurred in the years 1925 to 1927 and 1933 to 1936. During these later periods, there was a severe loss of fruit in Los Angeles and Orange counties, and a more moderate loss in Riverside, San Bernardino, Santa Barbara, Ventura, and San Diego counties.

Heavy infestations of the orange tortrix, as history indicates, have

been sporadic, so that a locality suffering serious damage one year might not have a recurrence of economic importance for several years.

DISTRIBUTION

The orange tortrix apparently is widely distributed in California (Essig, 1915) on various hosts. Lange (1936) reports it as feeding on the needles of pine in northern California. In southern California, it has been found in all of the citrus areas of importance in San Diego, Orange, Los Angeles, Ventura, Santa Barbara, Riverside, and San Bernardino counties. The localities of greatest abundance seem to lie in the region of the coastal influence; this includes most of Orange County and portions of San Diego, Los Angeles, Ventura, and Santa Barbara counties. The warmer and drier climate of the inland sections seems to limit the distribution; for in the large orange-producing localities of Riverside and Redlands, the moth rarely occurs in injurious numbers. The Corona district is an exception: heavy infestations have persisted there through the years 1933 to 1936, inclusive. Although this section is on the inland side of the Santa Ana Mountains, it is situated near the north end of the Santa Ana Canyon and possesses a climate more modified by the ocean than localities farther inland. The species is not of economic importance in the citrus sections of the San Joaquin, Sacramento, Coachella, and Imperial valleys.

Watson and Berger (1932) state that two or three species of tortricids occasionally drill tunnels into citrus fruit in Florida and specifically refer to "*Tortrix citrana* Fernald." However, Busck[7] states that he has never seen that species except from California and thinks the Florida record may be erroneous.

Bondar (1915) reported the orange tortrix as attacking oranges in Brazil, South America, but later (1929) he retracted the record and stated that the species attacking oranges in Brazil was *Gymnandrosoma aurantianum* Costa Lima.

Clemente (1929, p. 18) mentions three species of Lepidoptera as attacking oranges in Spain and refers to "*Tortrix citrana* Fer." as being found in the vicinity of Valencia. His description, in which he states that the larva of this species has a black head and that the moth is ash-gray, does not agree with our species of *Argyrotaenia citrana* (Fernald).

HOST PLANTS

The following list, compiled from literature and original observations, is a record of the known host plants of the orange tortrix. Because of the

[7] Information from personal correspondence with August Busck, January 24, 1933.

great variety of these plants, it seems logical to assume that there are many other plants on which the species may develop:

Acacia sp.
Aquilegia sp.
Aralia sp.
Asparagus plumosus
Asparagus Sprengeri
Begonia sp.
Brassica sp.
Chenopodium murale
Chrysanthemum maximum
Cineraria sp.
Citrus Limonia
Citrus paradisi
Citrus sinensis (Valencia and Washington Navel varieties)
Coix Lacryma-Jobi
Erodium sp.
Eucalyptus sp.
Euonymus sp.
Geranium sp.
Juglans californica
Juglans regia
Lactuca sativa
Lantana sp.
Lavandula sp.
Lotus sp.
Malva sp.
Nerium Oleander
Pelargonium sp.
Pentas sp.
Pinus radiata
Pittosporum eugenioides
Prunus Armeniaca
Quercus agrifolia
Rosa sp.
Salix sp.
Schinus Molle
Solanum Pseudo-Capsicum
Solidago californica
Tradescantia fluminensis
Urtica urens

DESCRIPTION AND BIOLOGY OF THE STAGES

Adult.—The adult orange tortrix (fig. 1) is a brownish- or buff-colored moth, with a saddle of a darker shade across the folded wings. The outline of the moth at rest widens rather rapidly from the head to the shoulders, and then runs back, flaring out a little at the tip of the wings like a bell. There is a slight indentation at the posterior end of the median line where the wings come together. The moths are about 10 mm long with a wing spread of about 16 mm. The male is smaller than the female and has a more slender abdomen. The males, 25 in number, from a brood of moths reared in the laboratory at a temperature range of 58° to 78° F averaged 9.82 mm in length from tip of palpi to wing tips when folded, and the females from the same brood, 16 in number, average 10.56 mm in length.

In the laboratory with a temperature range of 58° to 78° F, 25 males lived an average of 29 days on a diet of honey and water. The extremes of longevity were from 13 to 37 days. Under the same conditions, 15 females lived an average of 21 days with extremes of 12 to 42 days. The ordinary length of life without food is approximately from 8 to 10 days, which usually more than covers the time required for mating and egg laying.

The moths have not been observed in the act of feeding in nature. In the laboratory they freely take water or a solution of honey or sugar and water. It is not likely, however, that they seek the nectar of flowers, since

in nature they frequently issue at times when there are few, if any, flowers to furnish them with food. Water, no doubt, is frequently taken, and this may be had at any time of the year in the form of dew or rain. Food does not seem important to the adult, for in the laboratory apparently normal reproduction takes place among individuals which have not had food or water. Since individuals which have been fed live longer, the chances for the sexes to meet is increased when food or water is taken. This would be important when the populations became sparse.

In a miscellaneous lot of 162 moths, there were 77 males and 85 females, or a sex ratio of 0.52.[8] The mode of reproduction requires about an equal

Fig. 1.—Adults of the orange tortrix, *Argyrotaenia citrana* (Fern.): female (larger) and male. (× 3.5.)

number of males and females, for both sexes are short-lived, and ordinarily one male is likely to fertilize but one female. A male may fertilize more than one female, however. In a series of matings and rearings, the same male was mated with two different females. The first of these laid 168 fertile eggs, and the second laid 221 fertile eggs.

The moths are sexually mature when they issue from the pupae or soon thereafter. Table 1 is a record of 20 pairs and shows the time elapsed from emergence to mating and first eggs. In 6 cases in this series the females laid their first eggs within 24 hours after emergence. In nearly all of these matings the males are from 1 to 2 or more days older than the females. That is because the males issue earlier than the females, and sufficient males of exactly the same age as the females were not available for this experiment. In the case of pair number 5, however, both sexes issued at the same time and were mated, the first eggs being laid 24½ hours after emergence. Unfertilized moths sometimes lay a few scattered eggs which do not develop.

[8] Expressed as females to total population.

TABLE 1

Record of Twenty Matings of Orange Tortrix at 75° F and 70 Per Cent Relative Humidity

Pair	Sex and specimen number	Time from emergence to mating	Time from mating to first eggs	Time from emergence to first eggs, ♀	Time from first eggs to last eggs	Total eggs
		hours	*hours*	*hours*	*hours*	
1	♂ 1	43½	....	....	...	
	♀16	¼	47¼	47½	24	167
2	♂ 2	24¼	....	....		
	♀ 3	½	48	48½	24¾	237
3	♂78	144	....	....	...	
	♀ 4	½	23¼	23¾	24	238
4	♂ 5	43¼	....	....	...	
	♀19	¾	24½	25¼	94½	219
5	♂11	¼	....	....	....	
	♀ 7	¼	24¼	24½	22¼	237
6	♂ 8	24	....	....	....	
	♀21	½	53½	54	43¼	247
7	♂ 9	50	....	....	....	..
	♀18	¾	47¼	48	0	189
8	♂10	50	....	....	....	
	♀28	¾	22¼	23	24	177
9	♂12	50	....	...		
	♀29	¾	69¼	70	0	221
10	♂13	50	....	.		
	♀32	¾	47¼	48	0	236
11	♂70	66⅓	....			
	♀17	1/12	23 11/12	24	22¼	208
12	♂20	50	....	....	....	..
	♀33	¾	22¼	23	72	226
13	♂55	47¾	....	....	....	...
	♀22	¼	42	42¼	0	174
14	♂23	25½	....	....	....	...
	♀65	½	71¾	72¼	47¼	229
15	♂24	26¼	....	....	....	...
	♀51	½	93½	94	0	132
16	♂25	50¼	....	....	....	...
	♀58	¾	47	47¾	0	182
17	♂26	50¼	....	....		
	♀62	¾	46¾	47½	0	131
18	♂31	42¾	....	....	....	
	♀27	¾	47¾	48½	0	180
19	♂34	43½	....	....		
	♀67	¾	46¾	77½	101½	184
20	♂36	51¼	....	....	....	
	♀72	¾	46¾	47½	0	282

Oviposition takes place within a few hours after mating, and usually all of the eggs are laid within 2 or 3 days of that time. As shown in table 1, 11 of the 20 moths laid all of their eggs within 48 hours after emergence.

Moths preferably lay eggs on smooth surfaces. In the laboratory, eggs are laid on glass rather than on paper. In the field, the eggs are placed on foliage or fruit rather than on rough bark.

The number of eggs laid depends upon the size and vigor of the moths, and this depends upon the conditions under which they were reared. Thus, among moths grown at a temperature of 55° F there was a range of 153 to 428 eggs among the 37 females mated. The moth laying 153 eggs was 10.5 mm long and the smallest female of the lot. The one laying 428 eggs was one of a number of females 12 mm in length. Eighteen moths ranging from 10.5 to 11.0 mm in length laid from 153 to 338 eggs each, with an average of 248.8. Nineteen moths from 11.5 to 12.0 mm in length laid from 160 to 428 eggs each, with an average of 302.6 per female.

TABLE 2

ADULT INSECTS ATTRACTED TO DIFFERENT COLORED LIGHTS IN AN ORANGE GROVE, CORONA, 1935

Color	7 p.m. May 22 to 6 a.m. May 23		7 to 12 p.m. May 24		7 p.m. May 27 to 4 a.m. May 28	
	Argyrotaenia citrana	Other insects	*Argyrotaenia citrana*	Other insects	*Argyrotaenia citrana*	Other insects
Red*	131	266	50	219	56	261
White†	95	258	46	400	53	316
Blue‡	50	733	26	555	53	655

* Sixty-watt luminescent-type lamp.
† Sixty-watt incandescent-type lamp.
‡ One-hundred-twenty-watt luminescent-type lamp.

The moths prefer dark, shady places and consequently remain close about the foliage of trees and plants. A disturbance among the leaves of infested citrus trees may cause the adults to fly out with a short, quick flight and back into the foliage again.

The moths are negatively phototropic with reference to sunlight, but are often seen at night in the vicinity of lights. In the Corona district, red, white, and blue electric lights were placed in an orange grove where the orange tortrix population was high in the spring of 1935. Although other insects were more strongly attracted to the blue light, the orange tortrix showed a preference for the red light (table 2).

Broods of orange tortrix were reared at differences of 10° F from 35° to 95° F (table 3). Newly hatched larvae were placed in a temperature of 35°, but they were not able to develop because they apparently were numb from the cold and could not eat. Many lived longer than 3 weeks, but all slowly starved to death. At 45° a few adults developed,[9] and two

[9] Owing to a breakdown in the conditioning machinery, the brood at 45° F had to be transferred while in the fifth instar, and data on final development were not as complete as desired.

TABLE 3

DEVELOPMENT OF ORANGE TORTRIX AT DIFFERENT TEMPERATURES AND HUMIDITIES

Lot	Temperature, ° F	Relative humidity, per cent	Number started	Number matured	Mortality, per cent	Sex ratio*	Number of egg masses per pair	Eggs per mass	Eggs per pair	Eggs hatched, per cent	Development, in days			
											Eggs	Larvae	Pupae	Total cycle
1	35	70	54	0	100	0.00						.....		....
2	45	70	100	21	79	.62	12.50	16.00	190	....	56	123	56	236
3	55	90+	107	95	11	.48	4.75	58.00	276	83	29	51	25	105
4	65	70	104	93	10	.52	2.86	77.50	222	82	12	33	13	58
5	75	70	100	91	9	.46	4.50	45.24	203	78	7	21	9	37
6	75	35	50	39	22	.51	6.77	21.00	147	61	8	33	10	51
7	85	70	100	19	81	.37	....	....	......†	....	9	27	7	44
8	95	70	50	0	100	....	....	....	0	....	....	....	....	....
9	58–78‡		50	43	14	0.40	8.70	33.25	289	70	9	40	10	59

* Expressed as females to total population.
† Only one small mass of eggs produced by mating a female with a male from lot 3.
‡ Laboratory temperature.

pairs were mated and produced eggs. This temperature was evidently near the developmental zero. Strong broods were reared at 55°, 65°, and 75°. At 85°, the few moths procured were not able to produce eggs. However, one of these females was mated with a male from the brood reared at 55° and laid a few fertile eggs. Newly hatched larvae in a temperature of 95° took practically no food and all died before the end of the fourth day without reaching the second instar.

Field observations and the small amount of work done on the subject in the laboratory indicate that low relative humidity is less favorable to

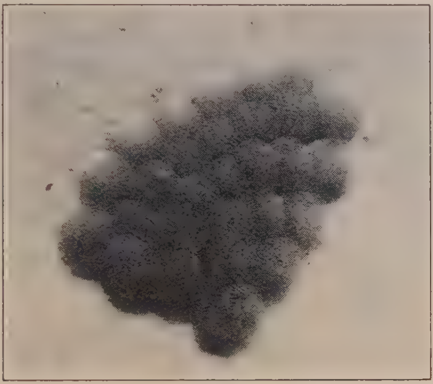

Fig. 2.—Eggs of the orange tortrix, *Argyrotaenia citrana* (Fern.) (× 11.8). (Courtesy of H. J. Quayle.)

the adults than high relative humidity. In the laboratory, the largest moths were produced at 55° F and 90 per cent relative humidity. Most of the rearings were made at 70 per cent relative humidity. At the temperature of 75°, one brood was reared at 35 per cent and one at 70 per cent relative humidity. The moths reared at the two relative humidities were about the same size, but those reared at 35 per cent relative humidity required a longer time for development and laid more but smaller egg masses and fewer eggs per female.

Egg.—The eggs are laid on the upper or lower surfaces of green leaves, on smooth green twigs, and on fruit in masses with each succeeding egg partly overlapping the preceding one. They are pale green to cream-colored when newly laid, but turn darker as the young larvae develop. The young embryos are readily seen progressing in development within the transparent shells. After the larvae have hatched, the mass of eggshells looks like a silvery patch on the leaf or stem on which it was laid.

The eggs are flat and oval in outline with a finely reticulate surface

(fig. 2). They vary somewhat in shape and size. Thus, 25 eggs from one moth averaged 0.91 mm in length and 0.69 mm in width, and 25 eggs from another moth averaged 0.92 mm in length and 0.75 mm in width. A lot of 17 eggs from several moths averaged 0.93 mm × 0.72 mm.

The number of eggs laid, number of masses, and number of eggs per mass under different conditions are recorded in table 3. Under favorable conditions, the eggs are laid in a few egg masses. When temperature or humidity or both are abnormal, the eggs are scattered in many small masses.

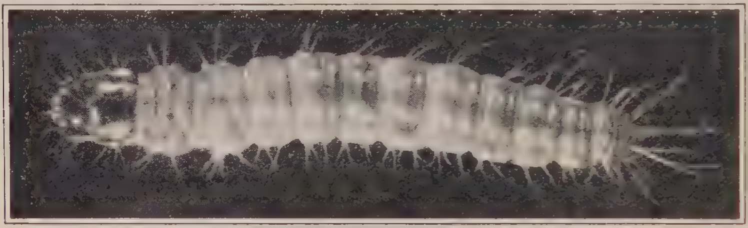

Fig. 3.—Last-instar larva of the orange tortrix, *Argyrotaenia citrana* (Fern.) (× 6).

The incubation period varies with the temperature (table 3). Under outside conditions, it may be as short as 8 days during the summer or as long as 20 days or more in winter.

The percentage of fertility under natural conditions seems to be near 100, for old egg masses found in the field are nearly always completely hatched. Of 1,077 eggs placed in trees in the field from matings in the laboratory, 83.3 per cent hatched; 10 per cent of the larvae died in the egg; 6.7 per cent were apparently infertile. For the percentage of hatch under different temperatures in the laboratory, see table 3.

Larva.—The newly hatched larvae are about 1.5 mm long. Full-grown larvae (fig. 3) are usually about 12 to 14 mm in length, but occasional individuals are as much as 16 mm long. The head and prothoracic plate are straw-colored, and the body is usually of the same color; however, greenish, dark-gray, or smoky-colored specimens are often found. The larvae are very active and wriggle away sideways or backwards when disturbed, or they may drop to the ground or hang suspended on a silken thread which they can ascend again. They are naked except for a few scattered hairs.

Orange-tortrix larvae are solitary, each making a nest for itself. As soon as the larvae leave the eggshells, they go in search of shelter and food. They are primarily leaf-rollers. The new growth of spring and the

bloom with it furnish the larvae with excellent food and shelter for a period of several months. Usually they locate in the young tips among the unfolding leaves, which they web together lightly for a temporary nest and on which they feed (fig. 4, *A*). They also often make nests among the buds and blossoms (fig. 4, *B*), and feed on the fresh buds and young

Fig. 4.—*A*, Tip of new shoot occupied by an orange-tortrix larva. The upper leaf is rolled together for the nest and adjoining leaves have been partly eaten. *B*, Nest made during the spring and composed of the parts from ten orange blossoms. When the nest was taken in October, it was occupied by an orange-tortrix larva 11 mm long and an *Apanteles* cocoon with a live pupa, indicating that a larva previously occupying the nest had been destroyed by the parasite.

ovaries of the blossom. When the blossoms fall, the dried petals and pistils collecting on leaves (fig. 5, *A*), or in fruit clusters (fig. 5, *B*), are webbed together and fastened to the leaf or fruit cluster to make nests that are occupied all summer or longer and often by several generations. In addition to this type of nest and food, many larvae locate under the sepals of newly set oranges and occupy the space around the receptacle between the upper part of the orange and the calyx. Here they feed on the surface of the orange just underneath the calyx. Other common locations for larvae are old, curled leaves, leaves webbed together, leaves touching fruits, and the small space between fruits in clusters. A single petal lying on a leaf or even the interior of a dried pistil from an old blossom may hide a small larva.

The normal food consists of tender foliage, but all stages of the fruit

from the undeveloped fruit in the buds to mature oranges may be fed upon. During the late summer and fall, orange-tortrix larvae are frequently found in nests of dead leaves and blossoms; in such cases, there is every indication that they have been feeding to some extent on this dead vegetation and slightly, if at all, on living plant food. This phenomenon occurs during periods of semidormancy which will be discussed later. Larvae found under such conditions were taken to the laboratory and reared to maturity on the dead vegetation in which they were found. To one set of these was given occasionally a drop of water, of which they

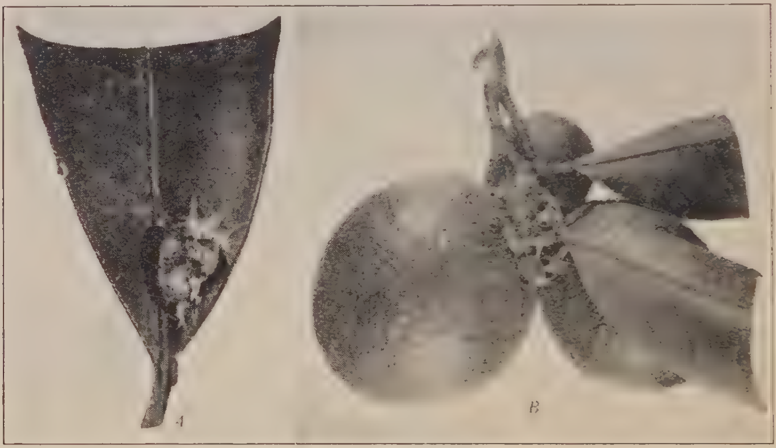

Fig. 5.—*A*, Nest on leaf. *B*, Nest in cluster of three oranges.

usually drank freely. To another set, no water was supplied, but after 45 days those surviving were fed green plant food until maturity. In the lot which was given water, but no green food, there were 13 specimens; 6 reached the adult stage, 1 succumbed after 115 days to an internal parasite which it had received in the field before collection, 2 were lost, and 4 died. The lot of 21 specimens receiving green food after no additional food or water had been given them for 45 days produced 4 adults; 7 succumbed to internal parasites which they had received in the field before collection, and 10 died. The deaths in both lots of the larvae not parasitized were probably due to starvation. The fact that some in each of these lots were able to reach maturity demonstrates the ability of the larvae to endure very severe conditions.

The number of larval instars varies from 5 to 7 or more, but under the most favorable conditions, it is presumably 5. Larvae reared at 55° F and 90 per cent relative humidity developed uniformly in five instars. The majority of those reared at 65° and 75°, with 70 per cent relative humid-

ity, also developed in 5 instars. At 75° and 35 per cent relative humidity, more than half of the larvae required 6 instars. At 85° and 70 per cent relative humidity, about one-third developed in 6 instars. In the laboratory with a temperature range of 58° to 78° (humidity not recorded), about 50 per cent developed in 5 instars, 40 per cent in 6 instars, and 10 per cent in 7 instars.

The constant-temperature developmental range of the larvae extends from slightly below 45° to slightly above 85° F. At 35° it was too cold for

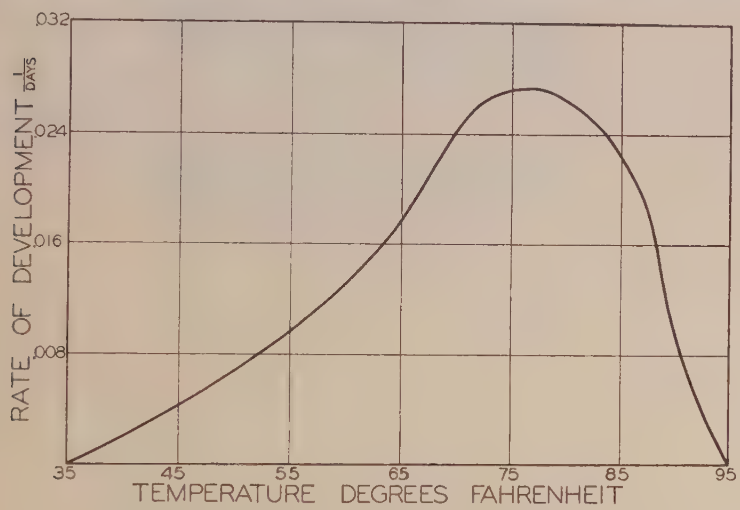

Fig. 6.—Rate of development (reciprocal of days required) of orange tortrix reared at constant temperatures.

the larvae to feed and they starved to death, and at 95° it was too hot and all larvae died before the end of the fourth day. At 45°, 78 per cent reached the pupal stage, and at 85° only 56 per cent reached the pupal stage. The rate of development at different constant temperatures is expressed in figure 6 and the time required to complete a life cycle under the same conditions is shown in figure 7.

At the laboratory temperature, there were about 24 hours of inactivity at molting time. When a larva finishes molting, it eats the old skin, except the head capsule, after which it feeds on fresh food during the remainder of the instar. Preparatory to pupation, the larva ceases feeding, surrounds itself with a small amount of webbing, and slowly transforms to a pupa. This stage (prepupal) lasts from 1 to 2 days in the laboratory.

The semidormancy previously referred to seems to be related to high temperature and low humidity. In the field, this condition occurs during

the latter part of the summer and early part of the fall. It is not comparable to estivation because there is not complete inactivity. However, activity is greatly reduced, and the larval period is lengthened much beyond that of the brood developing in later winter and early spring. Since there is not complete dormancy, some food must be taken, and that may consist of particles of the green foliage on which the nest is located or of the dried material composing the nest, as discussed in a former

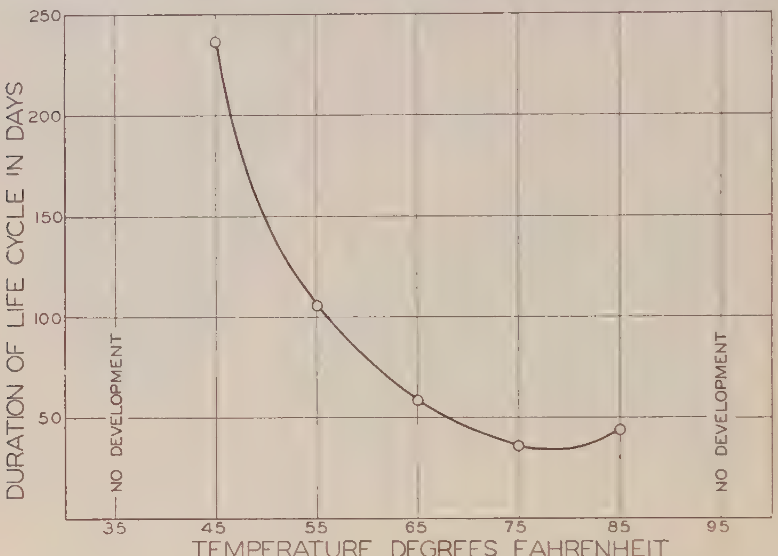

Fig. 7.—Duration of life cycle at different constant temperatures.

paragraph. Frequently lifting up a nest that rests on a green leaf exposes an irregular area where the larva has eaten the upper surface of the leaf.

In the interior districts of southern California, this delayed development is very pronounced, but it is less evident in the coastal areas. During the first week of June, 1934, young first-stage orange-tortrix larvae were present in a uniform brood in the Corona and La Verne districts. These larvae hatched about the latter part of May or first of June from eggs laid about the middle of May or a few days later. The average length of these larvae on September 10, over four months later, was only 4.8 mm. By November 14 they had grown to an average length of 10.0 mm, and the first pupae were found. Maximum pupation occurred about the first of January. Thus from hatching to pupation, this brood had a larval period of about seven months. Young larvae of the next generation ap-

peared about the first of March and reached pupation about the first of May, with a larval period of approximately two months.

In the laboratory, larvae reared at 75° F and 70 per cent relative humidity reached pupation in 20.9 days but larvae reared at 85° and 70 per cent relative humidity required 25.7 days. A change of humidity produced similar results. Thus, larvae grown at 75° and 70 per cent relative humidity matured in 20.9 days as stated above, but those at 75° and 35 per cent relative humidity required 29 days.

Fig. 8.—Dorsal (upper) and ventral (lower) view of pupae of orange tortrix, *Argyrotaenia citrana* (Fern.) (× 6).

Pupa.—The pupa (fig. 8) is light brown in color and about 8 mm long. The posterior end is pointed and the cremaster has eight small hooklets.

Pupation takes place in the last larval nest or location. The full-grown larva surrounds itself with a thin cocoon through which one may usually see first the larva in the prepupal stage and later the pupa. When the adult is about ready to emerge, the pupa often works itself to the outside of the nest, and the empty pupal skin is found on the outer edge or partly projecting from the nest.

The pupal period varies primarily with the temperature. Thus, it may be from 8 to 10 days during the summer and as long as 3 weeks during the winter months. In table 3 may be seen the time required for the pupal stage at various constant temperatures in the laboratory. The female pupa in all cases had a shorter development than the male pupa, although the larval and pupal period combined is longer for females than for males.

Humidity apparently also has some effect on the duration of the pupal period, although this may be an impulse from the effect of humidity on the larval development. At 75° F and 70 per cent relative humidity,

male pupae of 5-instar larvae required 219.4 hours and female pupae 198.2 hours, but at 75° and 35 per cent relative humidity, male pupae of 5-instar larvae required 262.3 hours and female pupae required 216.0 hours.

SEASONAL BIOLOGY

The most favorable conditions for the orange tortrix in southern California prevail through the cooler months, from November to June. During this period, the larvae are most vigorous, active, and well fed. They are more in evidence, present in greater numbers, and consequently do more damage than during the summer months. Development proceeds rapidly or slowly, according to the temperature, which is seldom extremely high during that portion of the year. Figure 9 shows the development of two succeeding generations under approximately outside conditions during the winter and spring.

The higher temperature and lower humidity of the late summer and early fall have an unfavorable influence on the development of the species. Under such conditions, the behavior of orange-tortrix larvae, as previously noted, borders on estivation. They do not become entirely inactive but feed little and develop slowly. Many of the larvae are gray or smoky in color and some appear starved, being rather emaciated and having heads as wide as the bodies or wider.

The inhibiting effect of temperature and humidity on the development is not so evident in localities near the ocean because the temperature is lower and the humidity is higher; yet even in these localities, considerable increase in activity is noticed after the rainy season begins.

In localities far enough removed from the coast, there are apparently two quite definite broods. For example, in the Corona district during the years 1934–1936, one brood developed in approximately three months, from about the middle of February to the middle of May. The second brood required about nine months, from the middle of May to the middle of February.

In the coastal belt, on the other hand, the infestations usually consist of individuals in various stages of development. In table 4 are shown data taken from October to March from an infestation in the Downey-Rivera district. Throughout this period the moth was present in various stages from egg to adult and there was no demarcation of broods.

In the interior localities, the spring brood is largely found in the new growth and among the flowers. The summer-fall brood is most commonly present during June and July as very small larvae under the buttons of young oranges. During the summer, such larvae move to the nests composed of old blossoms made by the previous generation and occupy these

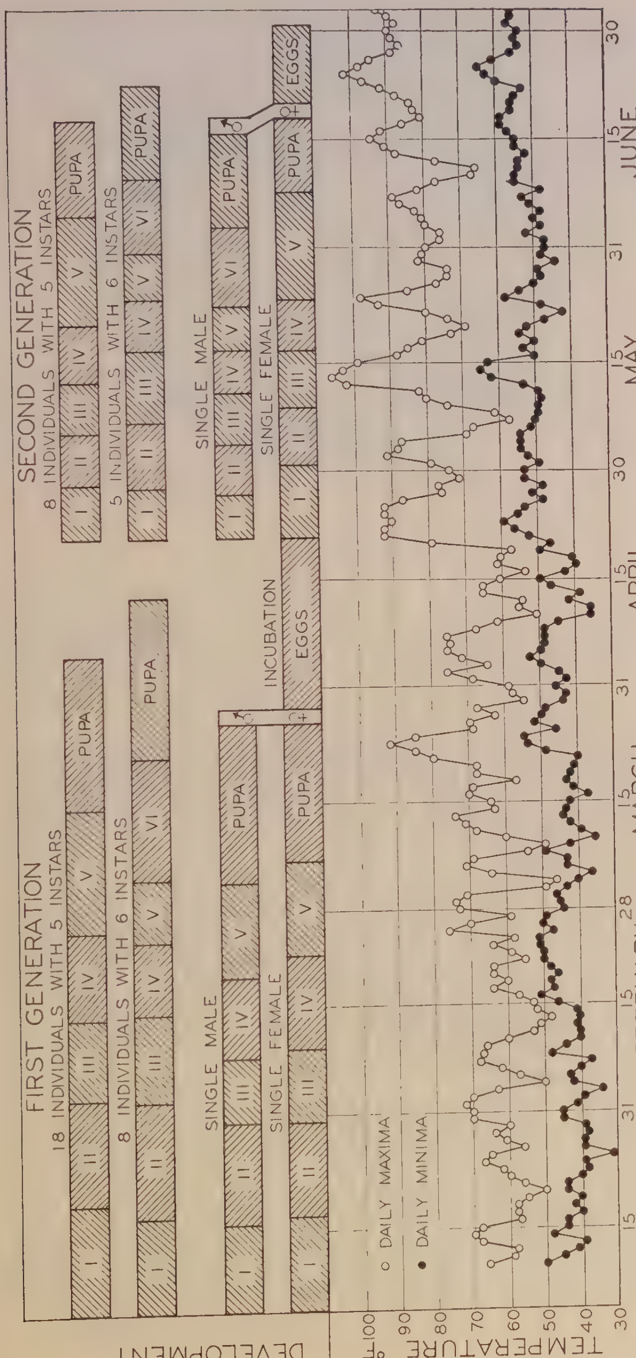

Fig. 9.—Development of two succeeding generations under lath-house conditions at Riverside, California.

nests in late summer and early fall, while in semidormancy. After the advent of cooler weather, usually associated with the first rains, they seek the fruit and may then be found in the clusters or among leaves touching the fruit.

In the coastal region where the generations overlap, the larvae occupy various locations at any given time. However, even in these localities, one is likely to find most of the individuals in the new growth in the spring, in the old larval nests during the summer, and among the fruits during the fall and winter.

TABLE 4

POPULATION OF ORANGE TORTRIX IN A VALENCIA ORANGE GROVE DURING A SEASON OF SEVERE DAMAGE TO THE CROP*

Date	Larvae			Pupae	Adults	Eggs	Parasites‡
	Small†	Medium†	Large†				
1933:							
October 9	73	36	44	26	4	3	11
November 20	56	44	36	1	1	2	15
December 27	39	62	41	2	0	1	5
1934:							
January 30	34	60	37	8	0	0	23
March 13	12	24	13	9	0	0	26
July 24¶	1	0	1	1	..	..	

* The data show the number found on four trees, 30 minutes per tree having been spent at each observation. The same trees were examined each time.

† Small, up to 5 mm in length; medium, 6 to 9 mm; large, 10 mm or longer.

‡ Refers only to parasites or their pupae found in the nest. The larvae were not dissected.

¶ Only one tree checked.

ECONOMIC IMPORTANCE

Although the larvae of the orange tortrix feed on the tender foliage of citrus trees and frequently on the petals and ovaries of buds and blossoms, their greatest damage is to the fruit, to which there are two principal types of injury—scarring, caused by superficial feeding of very young larvae while under the sepals or buttons of newly formed fruits (fig. 10), and deeper injuries, usually holes, into the fruit made by larvae of all sizes, and especially by those beyond the second instar (fig. 11).

Surface Injury to Fruit by Young Larvae and Its Effect on Size Grades and Premature Dropping.—Larvae that hatch in the spring, at the time new fruits are very small, find the space under the sepals or button of the fruit a most favorable place to live until they have grown too large for the small quarters. During this period, which extends more

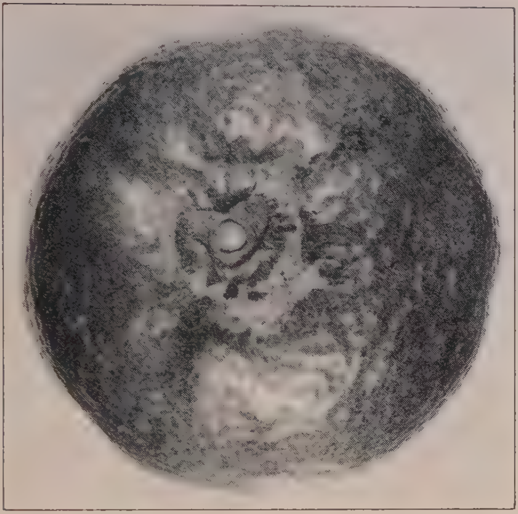

Fig. 10.—Scar made by small worm underneath the sepals while the fruit was small.

or less through the first and second instars, they feed by biting out very small particles from the surface of the orange peel, making injuries ranging from mere specks to irregular circles extending around the stem end of the fruit. As the fruit grows and presses closer to the sepals, the

Fig. 11.—Hole into fruit made by orange-tortrix larva.

larva, which has also increased in size, is too crowded and moves out to locate in a new place. Frequently small larvae also locate in the navel of the Washington Navel orange where they cause a similar type of injury. During the summer of 1934, 260 small larvae were taken from 572 fruits of this variety, and 15 of these, or 5.8 per cent, were in the navel. The remainder were underneath the button.

The injury made by the young larva in feeding on the surface of the fruit heals, and a russetlike scar resembling citrus-thrips injury is the

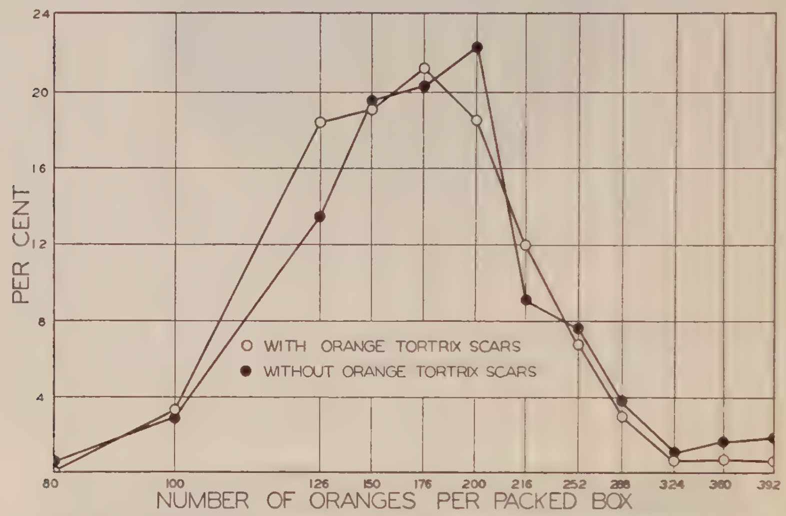

Fig. 12.—Effect of the presence of small orange-tortrix larvae under the sepals on the size of the mature fruit.

result. The scar made by orange-tortrix larvae is usually a little deeper and less broad and extensive in area than that made by the citrus thrips. As the fruit grows, the scar is no longer covered by the button and may be fairly conspicuous on the fruit at maturity. In moderate infestations, from 10 to 15 per cent of the fruit may be thus scarred, while in severe infestations as much as 85 per cent scarring has been observed.

The injury was originally thought to lower the grade of the fruit and also to stunt it in size and cause the so-called "pee-wee"[10] oranges (McGregor, 1934). Subsequent data (Basinger, 1936), however, have shown that the grade of the fruit is not likely to be greatly affected and that the scarring is not the cause of pee-wee oranges (fig. 12). This was determined by placing tags on newly set oranges in June, 1934, in groves where

[10] The so-called "pee-wee" oranges are those fruits which at maturity are usually too small to harvest.

young orange-tortrix larvae were abundant. The fruits were measured and the degree of injury, if any, noted at the time the crop was harvested in January, 1935. All of the tagged fruits remaining on the trees at the time of harvest were then run through the packing-house in a separate lot.

An examination of figure 12 shows that there is no significant difference in size between oranges injured by small larvae while under the button and those without such injuries. Both sets show a good percentage of average to large sizes and very few small oranges. This conclusion is borne out by an examination of a lot of pee-wee Washington Navel oranges selected at random in a grove where the percentage of scarring by small orange-tortrix larvae was high. It was found that in a lot of 254 pee-wee oranges, 46 per cent bore no trace of orange-tortrix injury and that 54 per cent had various degrees of injury from a mere trace to a more or less complete ring around the button.

The scarring had no appreciable effect on the grade in the Corona district, where the packing-house made four grades of oranges: Fancy, Choice, Standard, and Cull. At La Verne, one house was packing five grades: Extra Fancy, Fancy, Choice, Standard, and Cull. Through this house was run in the normal procedure a lot of 529 mature Washington Navel oranges from an infested grove in that district. Oranges were selected which bore the more conspicuous type of orange-tortrix scar but otherwise represented Extra Fancy and Fancy fruit as nearly as one could judge from the unwashed fruit on the trees. The lot was graded as follows:

	Number	Per Cent
Extra fancy	204	38.56
Fancy	313	59.17
Choice	9	1.70
Standard	3	0.57
Cull	0	0.00

In this lot of fruit, each of which had a scar larger than the average, the effect on the grade, if any, was slight since it actually packed nearly 98 per cent Fancy and Extra Fancy.

The presence of small larvae under the buttons, their injury to the fruit, and perhaps also to the lower portion of the button, and the attendant light webbing and frass did not increase the premature dropping of infested fruits over those bearing no orange-tortrix injury. From a total of 1,122 fruits with larvae present under the buttons in June, 1934, 177, or 16.0 per cent, dropped before harvest in January, 1935, whereas out of a total of 730 fruits without larvae present under the buttons at the same time, 111, or 15.2 per cent, fell off before harvest.

Effect of Deeper Injuries to Fruit on Grade and Premature Dropping.—The deeper injuries to the fruit, on the other hand, cause a definite loss. The most common type of deep injury is a hole through the peel into the juice cells. Such holes are made by larvae of all sizes, but usually the larvae of the first and second instars prefer tender tips, blossoms, or as described above, the surface of the skin of the newly set fruit. Fruits with holes to the flesh soon start to decay and drop off. Holes made in green oranges by orange-tortrix larvae cause the fruits to color prematurely. The area around the injury yellows first, then gradually the entire fruit becomes more highly orange-colored than the surrounding fruits. During wet weather, the decay is very rapid and fruits frequently decay on the tree and remain hanging there, drying into mummies.

Holes made by small larvae are called "pin-hole injuries" and are hard to detect by graders in the packing-house. When damaged fruits are packed, they decay in the packed box. Holes may be made through any part of the surface of the orange, in the navel end, and under the sepals, but the most common point of injury is on the side at about the middle line or toward the stem end, known as the "shoulder." This is the most common point of contact when fruits touch each other in clusters. At such a location the orange-tortrix larva makes a nest by webbing together fallen blossoms or leaves collected there, or by simply fastening a few strands of web between the touching fruits. Fruits hanging singly are less subject to damage, but these are often in contact with leaves that may be webbed to the fruit to form a nest, underneath which the larva feeds on the fruit.

Injuries to the rind only may not cause the fruit to drop, but usually such fruits are culled out at the packing-house. An injury to the rind of a green orange is often followed by a thick white exudation which fills up the cavity and hardens. The wound may then heal and the fruit remain on the tree apparently recovered, though it is marred sufficiently to lower it materially in grade. Injuries to the rind of mature oranges, especially during the summer and fall, are often followed by brown, leathery spots. Other injuries and conditions also cause brown spots on citrus so that not all brown spots can be attributed to orange-tortrix injury. Washington Navel oranges are scarcely affected by this type of injury because they are harvested before the beginning of summer.

The amount of damage which an orange-tortrix infestation may do can be ascertained only by a comparison of the damaged[11] fruit with the entire

[11] Refers to injuries which cause the fruit to fall from the tree, decay, or be classed as culls.

crop. To accomplish this, a record of all of the fallen fruit must be kept from the time the crop is set until it is harvested. To procure these data, all of the fallen fruits must be picked at frequent intervals and the number of oranges damaged by orange-tortrix larvae, as well as those having fallen from other causes, must be noted. The number of damaged fruits still on the trees at the time of harvest must also be determined.

The damage to a Valencia crop may be greater than that to a crop of the Washington Navel or other variety of oranges, because Valencias are

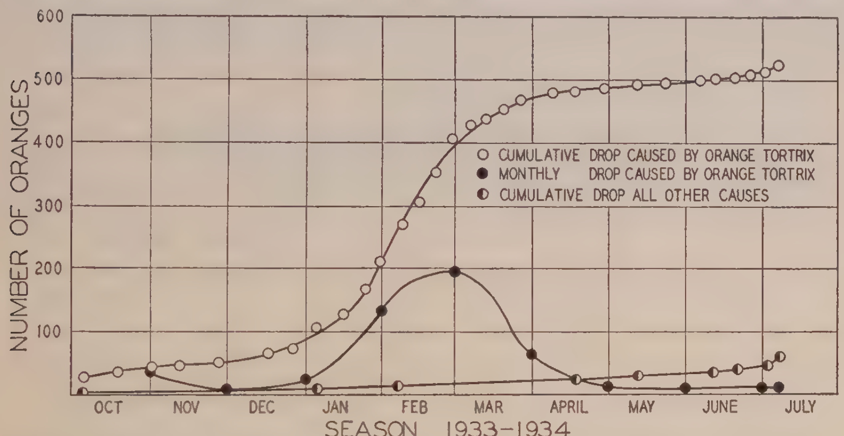

Fig. 13.—Damage caused by a very heavy infestation of orange tortrix to a Valencia orange crop. Only the fallen fruits are represented by the graph.

on the trees for a longer time. Although both the Valencia and Washington Navel orange bloom and set their crops in the spring, they mature at different times. The navel orange is harvested from December to May, and the Valencia is harvested from May to November. Thus, the navel crop may be subject to worm damage for a maximum of about 12 months (counted from the setting of the fruits) and the Valencia crop for a maximum of about 18 months.

The most detailed data obtained on the amount of damage an orange-tortrix infestation may do to a Valencia crop were taken in a grove near Downey, Los Angeles County, during the season of 1933–34. Damage was first evident in this grove about September, 1933, but the counting of fallen oranges was not begun until about the first of October. Though most of the oranges injured prior to October were obtained when the fruit was first picked up, the actual damage was somewhat higher than the figures obtained from the data. Beginning with October 5, 1933, and continuing to harvest on July 9, 1934, all of the fallen fruits were taken up at regular intervals from 20 trees divided into 4 groups of 5 trees

each in different locations in the grove. The data are shown in figure 13. Owing to orange-tortrix injury, an average of 522 fruits per tree fell to the ground from the 20 trees, and an additional 171 fruits per tree injured[12] by the orange tortrix were hanging at harvest time, making a total of 693 fruits per tree lost because of orange-tortrix injury. These trees produced a total crop of 34,296 oranges and lost 13,861, or 40.42 per cent, by orange-tortrix damage. The figures show what may be done by an unusually heavy infestation.

Table 5 presents a summary of the data obtained from seven trees in a Washington Navel grove at Escondido, San Diego County, during the

TABLE 5

SUMMARY OF DAMAGE TO WASHINGTON NAVEL ORANGES, RECORD FROM SEVEN TREES, ESCONDIDO, 1925

Tree	Number of oranges		Per cent of fruit damaged
	Total crop	Damaged by larvae	
L 10*	1,796	574	32
K 11	815	219	27
K 12	1,152	289	25
K 13	1,403	178	13
K 14	737	128	17
K 15	1,445	252	17
K 16	1,196	153	13
Total	8,544	1,793	21

* L 10 was selected as the most heavily infested tree in the grove.

fall and winter of 1925–26. The infestation was heavy and practically all of the damage, which averaged 256 oranges per tree, occurred from about the middle of October to January 26 when the crop was harvested. During the twelve succeeding years, no infestation of equal severity has occurred in this grove.

POPULATIONS OF ORANGE—TORTRIX LARVAE

The number of orange-tortrix larvae per tree necessary to cause appreciable damage is far less than the number of many other insect pests necessary to constitute infestations of economic importance. No damage to the crop of mature orange trees results from the presence of scale insects or aphids until actually thousands of individuals are present. In the case of the orange tortrix, however, a population of 50 to 100 or more larvae on a twenty-year-old orange tree would be considered a heavy infestation.

[12] Only injuries causing a total loss of the fruit are considered here.

In making a field estimate of an orange-tortrix population, it is assumed that the infestation is uniform over the entire tree and that in searching for larvae one can find 75 per cent of the individuals actually present. Therefore, $\frac{4}{3}$ times the number found, divided by the portion of the tree searched, equals the estimated population of the entire tree. Since most bearing trees are larger than can be thoroughly gone over from the ground, the portion of the tree searched in working around the tree from the ground is estimated. If one-third of a tree is searched and 30 individuals are found, the tree has a population of $\frac{\frac{4}{3} \times 30}{\frac{1}{3}}$, which is 120. Table 6 shows some tree estimates made in a grove where damage was severe.

The number of individuals found in a given period of time proved a reliable index in determining the degree of an infestation. The efficiency of this method of evaluating populations of orange tortrix depends upon the experience of the one making the examination. It was found that persons unfamiliar with the various stages and habits of the moth could, within a few days, acquire proficiency in locating and identifying the various stages of the species.

TABLE 6

Estimated Number of Larvae per Tree of Known Heavy Infestations of Orange Tortrix

Date	Locality	Number of trees searched	Estimated portion of each tree searched	Average number of larvae found per tree	Average estimated larval population per tree
1923:					
October 9	San Marino	2	⅓	12	48
1924:					
January 8	San Marino	6	⅓	11	44
February 28	San Marino	3	⅓	15	60
May 12	San Marino	2	⅓	43	172
May 21	Covina	2	⅓	20	80

When the larvae are actively feeding on the fruit, the presence of an infestation is conspicuous because of the damaged fruit. However, a high population of orange tortrix may be present, particularly in the interior districts, during the late summer and early fall with scarcely a trace of damage to the fruit. To discover an infestation and obtain data on the relative abundance of the individuals under such conditions requires the greatest amount of patience and careful observation.

Experience has shown that if an observer finds 15 or more orange

tortrix per hour during the late summer and early fall, the population is sufficiently dense to cause moderate to severe damage to the crop. For example, on September 9, 1926, 2 hours were spent in examining a grove at Escondido and 4 orange-tortrix larvae were found. These were from 3 to 5 mm long and were not feeding on the fruit. This indicated a very small orange-tortrix population and subsequently during the fall and winter the grove had a negligible amount of damage. On September 14, of the same year, 2¼ hours were spent in a grove at Anaheim and 50 larvae and 3 pupae were found. Most of the larvae were small and not damaging the fruit, but were present in old, curled leaves, bunches of old, fallen blossoms, and under the buttons or sepals of green oranges. The population represented by this number proved sufficient to cause serious damage. Injured oranges began to drop to the ground about the last of October and this continued through November, December, and January. In October, 1933, an unusually heavy infestation of orange tortrix was found in a Valencia grove in a coastal district. A population check was made on 4 trees timed to 30 minutes per tree. An average of 39.8 living larvae and pupae per tree were found in the time allotted. During the season, these trees lost an average of 597.5 fruits per tree from orange-tortrix damage.

The size of the crop should also be taken into consideration in judging the effect of an infestation. The same number of orange-tortrix larvae will do more damage to a good crop than to a light crop because fruits are closer together and more in clusters.

OTHER SPECIES THAT MAY BE PRESENT

Often *Holcocera iceryacella* and the orange tortrix are present in the same trees. *Holcocera iceryacella* is more abundant in the coastal belt than in interior districts, and damage to oranges by this species usually occurs during the summer and fall. Washington Navel oranges are practically undamaged by *Holcocera iceryaecella*. The larvae are grayish-brown with shiny dark-brown head capsules.

Platynota stultana is much less common but is similar in habits to the orange tortrix and may be grouped with the latter for practical purposes in rating infestations. First-instar larvae of *Platynota stultana* have a dark head capsule in contrast to the light-colored head capsule of the orange tortrix. Other larval stages of the two species are indistinguishable in the field.

Pyroderces rileyi has been found in citrus only in San Diego. Its habits are somewhat like *Holcocera iceryacella*, but it is readily distinguished from the latter by the pinkish color of its larvae.

NATURAL ENEMIES

The natural enemies of the orange tortrix are very important in keeping this pest from being far more serious than it now is. Twelve primary parasites are recorded (Basinger, 1935), but only four of these, *Apanteles aristoteliae* Viereck, *Hormius basalis* (Prov.), *Exochus* sp., and *Campoplex* n. sp., have been found to be of outstanding importance during this investigation. The orange tortrix frequently increases to sufficient numbers to do considerable damage, and in certain localities seems to be persistent for several years at a time; nevertheless, whenever a sample of tortrix material is taken in the field, regardless of the time of

TABLE 7

PARASITIZATION OF ORANGE TORTRIX IN THE ESCONDIDO INFESTATION OF 1925

Date	Larvae dissected	Per cent parasitized
November 19	88	26
November 27	45	46
December 17	48	52
January 7	15	73
May 19	11+3 pupae*	90

* Although only 11 larvae and 3 pupae were found on this date, the number of larvae represented by counting the parasite cocoons found in orange-tortrix nests was 50.

year, some parasitized individuals are almost certain to be present. The progress of parasitization in a pure infestation of orange tortrix was conspicuous in the Escondido district in 1925 (table 7). This infestation was incipient about the early part of October, at which time parasitization undoubtedly was very low. On November 19, parasitization was only 26 per cent and much damage had already been done to the orange crop, but parasitization rose so rapidly after the middle of November that only a small portion of this brood reached maturity; the succeeding generation of orange tortrix was so overwhelmed with parasites that no further damage occurred to the crop during that season, nor during the following season.

Although five secondary parasites are recorded from the various primary parasites of the orange tortrix, the author has never found any one or all of them together abundant enough to affect seriously the value of any of the primary parasites.

Apanteles aristoteliae Viereck (fig. 14) is the most common natural enemy of the orange tortrix in southern California. The species (Viereck, 1912) is, according to Muesebeck (1920), synonymous with *Apanteles*

(*Apanteles*) *gelechiae* Viereck (Viereck, 1912). Coquillett (1894) reported two parasites reared from the orange tortrix in California. One was a dipterous parasite, probably a tachinid, and the other, by his description, undoubtedly was *Apanteles aristoteliae*.

In addition to the orange tortrix in California, the recorded hosts and localities are: *Aristotelia fungivorella*, Anglesea, New Jersey (Viereck,

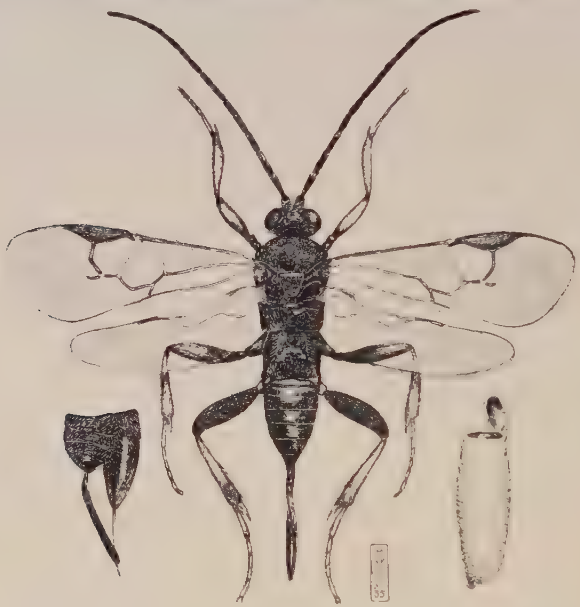

Fig. 14.—*Apanteles aristoteliae* Viereck, adult (× 12) and cocoon (× 3). (From Quayle, *Citrus and Other Subtropical Fruit Insects*, by permission of the Comstock Publishing Co., Inc.)

1912); *Gelechia trialba-maculata*, East River, Connecticut (Viereck, 1912); *Gelechia confuselle*, Benton Harbor, Michigan (Muesebeck, 1920).

The parasite is about 3 mm in length. It is black with filiform antennae about as long as the body. The wings are clear except for the light-brown stigma. It is a solitary internal parasite, although it concludes the last few moments of its larval development by feeding externally after having emerged from the body of the host.

Host larvae are attacked in all stages, the parasite having been found present in orange-tortrix larvae from 2½ to 14 mm in length. The parasite is more frequently found, however, in larvae which are less than half grown. At laboratory temperature, the life cycle from egg to adult requires about 25 days.

The behavior and development of the parasite is best shown by the following typical cases at laboratory temperatures. On May 20, an *Apanteles* adult was put into a cage with a large orange-tortrix larva, 14 mm long. The parasite, upon discovering the host, made a very aggressive attack, in spite of the host's violent movements. The attack and oviposition were accomplished in a second or two, and the orange-tortrix larva, though greatly excited, showed no indication of paralysis after the attack. On June 6, a parasite larva emerged from the host, the egg and larval stages requiring 17 days. On June 9, an orange-tortrix larva 3 mm in length was taken from the field to the laboratory, where it was kept supplied with food. This larva had been parasitized in the field prior to capture, as subsequent developments disclosed. On July 2, when examined, a parasite larva had just emerged and was maneuvering to get a hold on the body of the host. This was shortly accomplished, the parasite fastening its mouth parts near the posterior end of the host. The host was not yet dead, as could be seen by the movement of its head and legs. The parasite larva absorbed the body juices rapidly and in half an hour only the drawn-up skin of the host was left. Pushing this to one side so that it would not be in the way of the cocoon, the parasite immediately began to weave a web around itself. On the following morning the cocoon was completed. Development of the egg and larva required 23 days, and in addition the time from parasitization in the field to the time the host was collected. The longer time required over the preceding case was undoubtedly due to the much smaller size of the host larva at the time of parasitization; for temperatures were warmer during the latter case than in the former.

A full-grown *Apanteles* larva reaches a length of 5 mm and is about 1½ mm thick. The cocoon (fig. 14) is white, solidly woven, ovoid, and about 3 mm in length. It is found in the nest formerly occupied by the host. The duration of the pupal stage is more dependent on temperature than the larval stage, since the pupa occurs outside of the host. In a typical case in the laboratory, a cocoon was completed on June 15 and the adult issued on June 23, the pupal stage requiring 8 days. At outside temperatures, a cocoon was completed on December 8, and the adult issued on December 29, the pupal stage requiring 21 days. The fully developed adult within the cocoon cuts out a circular disk for its exit. Often cocoons are found with these disks still attached on one side like miniature doors.

Hormius basalis (Prov.) (fig. 15) is probably second in importance as a parasite of the orange tortrix. Specimens were sent to L. O. Howard in March, 1924. He referred the parasite to A. B. Gahan for determina-

tion, and on June 10, 1924, wrote as follows: "Mr. Gahan now reports that the parasite is *Hormius basalis* Prov., described by the French Canadian as *Zele*. It has never been transferred to *Hormius* in literature, but Gahan saw the type in Montreal in 1915 and recognized it as *Hormius*."

The species is an external parasite. The eggs are deposited in the web of the host nest and the young parasites attach themselves to the host

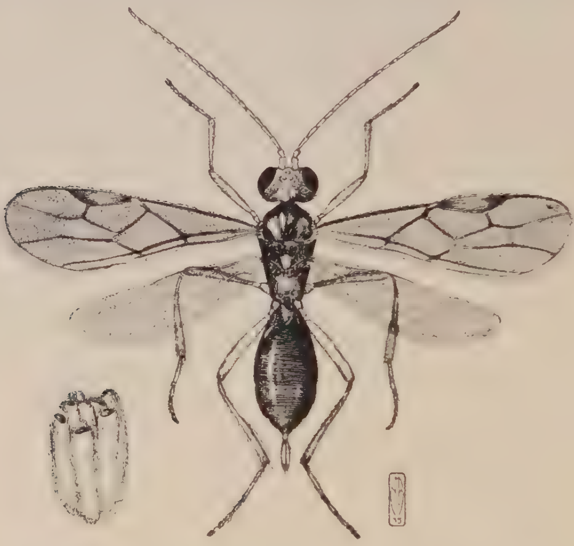

Fig. 15.—*Hormius basalis* (Prov.), adult (× 13) and cocoons (× 3). (From Quayle, *Citrus and Other Subtropical Fruit Insects,* by permission of the Comstock Publishing Co., Inc.)

when the latter comes in contact with them. The host soon surrounds itself and the attached parasites with a web and becomes inactive. When the parasite larvae are ready to pupate, they spin elongated cocoons frequently arranged lengthwise in one group like a pile of posts (fig. 15). As many as eight are known to develop on a single host.

The adult is slightly less than 3 mm in length. The body is yellowish brown, the eyes dark, and the wings clear except for a clouded stigma.

The eggs are cylindrical, a little more pointed at one end than at the other, translucent, almost smooth, shiny, whitish, and about 0.14 mm × 0.42 mm in size.

A life cycle in outside temperatures at Riverside extended from November 23 to January 11, exclusive of the incubation period.

Exochus sp. (fig. 16) was found in considerable abundance in the years 1933 to 1935. The egg of the parasite is inserted into the body cavity of the host larva and the adult parasite issues from the host pupa. The parasite occurs in both the coastal and interior localities and is most common from February to June.

Apanteles aristoteliae and *Hormius basalis* and other parasites make their cocoons in the nest of the host; therefore, an examination of the

Fig. 16.—*Exochus* sp. adult (× 6), and orange-tortrix pupa (× 2) from which the parasite issued. (From Quayle, *Citrus and Other Subtropical Fruit Insects,* by permission of the Comstock Publishing Co., Inc.)

older nests of the orange tortrix will give data on the relative abundance of these species. Such data were obtained from various localities during 1924 to 1927 inclusive. About 75 per cent of the parasites represented were *Apanteles aristoteliae* and 13 per cent were *Hormius basalis*. The remaining 12 per cent consisted of all other parasites of the host.

SUMMARY

The orange tortrix described in 1889 by Fernald as *Tortrix citrana* is now considered to belong to the genus *Argyrotaenia.*

The species is probably native to the extreme southwestern United States and perhaps to contiguous Mexico.

It was first reported injurious to citrus in 1885 in southern California, and since that time infestations have appeared sporadically every few years in the principal citrus sections in the southern part of the state.

Distribution extends from southern to northern California, but the localities of greatest abundance seem to be in the region of the coastal influence of the southern part of the state. Records of the species in Florida and Spain are not well substantiated.

The recorded host plants total forty species of great variety and include both native and introduced plants.

The adult orange tortrix are buff-colored, about 10 mm in length, and have a wing spread of about 16 mm. They live from 8 to 10 days without food and from 2 to 3 weeks when fed. They are negatively phototropic but show some attraction to electric light, especially red. They are apparently sexually mature when they issue from the pupae. Mating and oviposition take place within a few days after the adults issue. The number of eggs laid depends on the conditions under which the adults are reared. At 65° F constant temperature, the moths laid an average of 222 eggs per pair.

The eggs are flat, oval in outline, and approximately 0.7 × 0.9 mm. They are laid on smooth surfaces like the upper or lower surface of a leaf. The incubation period varies with the temperature, being from 8 to 10 days in summer and 20 days or more in winter under outside conditions.

The larvae are usually straw-colored. They are about 1.5 mm long when hatched and 12 to 14 mm long when mature. On citrus they normally feed on the tender growth, buds, and fruit, but under certain conditions may subsist on dead vegetation. There are from five to seven larval instars. The constant-temperature range of development extends approximately from 45° to 85° F. Constant temperatures of 55° to 75° with 70 per cent relative humidity proved very favorable to the larvae. Low relative humidity and high temperatures tend to retard development. In the interior districts, many larvae are semidormant through late summer and early fall.

The pupa is light brown and about 8 mm long. It is usually surrounded by a thin cocoon. Pupation takes place on the tree in the last larval nest. The pupal period under outside conditions is from 8 to 10 days in summer and up to 3 weeks or more in winter.

The orange tortrix is of economic importance to citrus because of the damage it does to the fruit. This damage consists of scarring, which is of minor importance, and of eating holes into the fruit, which means the total loss of the fruit. In one case 40 per cent of the crop of Valencias was lost owing to orange-tortrix damage.

The most favorable seasonal conditions are those existing from November to June. In the Corona district, there are two broods. The spring brood requires about three months, and the summer-fall brood about nine

months. In the coastal areas, all stages may be present at any given time with no indication of broods.

From 50 to 100 or more larvae on a twenty-year-old orange tree may be considered a heavy infestation. Estimated larval populations on heavily infested trees ranged from 44 to 172. Data on the relative density of an infestation can be obtained by counting the number of individuals found in a given period of time. If an experienced observer finds 15 or more orange tortrix per hour, the infestation may be said to be moderate to severe. As many as 80 living larvae and pupae have been found per hour in an infestation where there was an unusually great loss of fruit.

The species *Holcocera iceryaeella, Platynota stultana,* and *Pyroderces rileyi* may be in the same trees with *Argyrotaenia citrana.*

There are twelve recorded primary parasites and five secondary parasites. The most common primary parasites are *Apanteles aristoteliae, Hormius basalis, Exochus* sp., and *Campoplex* n. sp. The parasites seem generally distributed with the orange tortrix and serve as a severe check to the host. The secondary parasites have not been found in great abundance during this study.

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LITERATURE CITED

BASINGER, A. J.

1935. Parasites reared from *Argyrotaenia (Tortrix) citrana* Fernald. California State Dept. Agr. Mo. Bul. 24(4, 5, 6): 233–34.

1936. Notes on the orange worms, *Argyrotaenia (Tortrix) citrana* Fernald and *Platynota stultana* Wlsm. Jour. Econ. Ent. 29(1): 131–34.

BASINGER, A. J., and A. M. BOYCE.

1935. Progress report on orange worm control. California Citrograph 22(6) 158, 178–79.

1936. Orange worms in California and their control. Jour. Econ. Ent. 29(1): 161–68.

BONDAR, G.

1915. Insectos damninhos á agricultura. Fasciculo iii—Pragas das laranjeiras e outras auranciaceas. [Insects injurious to agriculture. Part III—Pests of orange trees and other aurantiaceae.] 47 p. Duprat & Co. São Paulo, Brazil. *Abstracted in:* Rev. Appl. Ent., Series *A,* 4:201. 1916.

1929. Insectos damninhos e molestias da laranjeira no Brasil. [Diseases and insect pests of oranges in Brazil.] Bol. Lab. Path. Veg., Bahia, 7:1–79. *Abstracted in:* Rev. Appl. Ent., Series *A,* 18: 173. 1930.

CHAPPELOW, WILLIAM.

1898. Injury by the orange leaf-roller. p. 99. *In:* Howard, L. O. Some miscellaneous results of the work of the Division of Entomology, III. U. S. Dept. Agr. Div. Ent. Bul. 18 (n.s.): 1–101.

CLEMENTE, FREDERICO GOMEZ.

1929. El *Cryptolaemus montrouzieri* Muls. parasito del *Pseudococcus citri* Risso. [*Cryptolaemus montrouzieri* Muls., a parasite of *Pseudococcus citri* Risso.] 47 p. Estación Regional de Patologia Vegetal. Valencia, Spain.

COQUILLETT, D. W.

1894. Report on some of the injurious insects of California. The orange leaf-roller (*Tortrix citrana* Fernald). p. 24. *In:* Riley, C. V. Reports of observations and experiments in the practical work of the division. U. S. Dept. Agr. Div. Ent. Bul. 32 (o.s.): 1–59.

ESSIG, E. O.

1915. Injurious and beneficial insects of California. California State Printing Office, Comm. Hort. Mo. Bul. Sup. 2nd ed. *lxxxi* + 541 p. (See specifically p. 441.)

FERNALD, C. H.

1889. North American microlepidoptera, *Tortrix citrana* n. sp. Entomologica Americana 5(1): 18.

LANGE, HARRY W.

1936. The biology of the orange tortrix, *Eulia (Argyrotaenia) citrana* Fern. California State Dept. Agr. Mo. Bul. 25(2): 283–85.

McGregor, E. A.
1934. *Platynota stultana* Wlsm. (Lepidoptera) damaging green oranges in southern California. Jour. Econ. Ent. 27(5):974–77.

Muesebeck, C. F. W.
1920. A revision of the North American species of ichneumon flies belonging to the genus *Apanteles*. U. S. Natl. Mus. Proc. 58(2349): 483–576. (See specifically p. 522.)

Quayle, H. J.
1910. The orange tortrix (*Tortrix citrana* Fernald). Jour. Econ. Ent. 3(5): 401–403.
1918. The orange tortrix, cause of decay. California Citrograph 3(6): 133.

Viereck, H. L.
1912. Contributions to our knowledge of bees and ichneumon flies, including the descriptions of twenty-one new genera and fifty-seven new species of ichneumon flies. U. S. Natl. Mus. Proc. 42(2882):613–48. (See specifically "*Apanteles (Apanteles) aristoteliae*, new species," p. 613, and "*Apanteles gelechiae*, new species," p. 615).

Watson, J. R., and E. W. Berger.
1932. Citrus insects and their control. Florida Agr. Ext. Ser. Bul. 67:1–140. (See specifically p. 107–108.)

Weldon, G. P.
1914. Insect notes. California State Comm. Hort. Mo. Bul. 3(3): 168.